UNIVERSITÉ DU QUÉBEC À TROIS-RIVIÈRES

en association avec

UNIVERSITÉ DU QUÉBEC À MONTRÉAL

FACTEURS IMPLIQUÉS DANS LA STRUCTURATION SPATIALE ET L'INTÉGRITÉ ÉCOLOGIQUE DE LA PERCHAUDE DANS UN LAC FLUVIAL

THÈSE

PRÉSENTÉE

COMME EXIGENCE PARTIELLE

DU DOCTORAT EN SCIENCES DE L'ENVIRONNEMENT

PAR

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DÉCEMBRE 2010

UNIVERSITÉ DU QUÉBEC À TROIS-RIVIÈRES

DOCTORAT EN SCIENCES DE L'ENVIRONNEMENT (PH. D.)

Programme offert par l'Université du Québec à Montréal (UQAM)

en association avec

l'Université du Québec à Chicoutimi (UQAC)
l'Université du Québec à Rimouski (UQAR)
l'Université du Québec en Abitibi-Témiscamingue (UQAT)
et l'Université du Québec à Trois-Rivières (UQTR)

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Thèse soutenue le 12/11/10

AVANT-PROPOS

Les chapitres I, II, et III de cette thèse sont présentés sous forme d'article scientifique. Je confirme avoir rédigé toutes les versions des articles présentés dans ma thèse et intégré les commentaires de mes co-auteurs suite à leur lecture des manuscrits. En ce sens, ma contribution à la rédaction de ces articles a été majeure. Le premier chapitre a été publié dans le périodique *Wetlands* et a été écrit en collaboration avec les Dr Pierre Magnan et David Marcogliese (Bertrand *et al.* 2010). Le deuxième chapitre a été écrit en collaboration avec les Dr Pierre Magnan, David Marcogliese et Gilbert Cabana et a été soumis au périodique *Journal of Animal Ecology*. Quant au troisième chapitre, il a été écrit en collaboration avec les Dr Pierre Magnan et David Marcogliese et sera soumis au périodique *Aquatic sciences*.

REMERCIEMENTS

C'est avec beaucoup de gratitude que je franchis cette étape de ma vie. Gratitude envers la vie qui m'a donné la chance de naître dans une société qui offre, encore, la possibilité de s'instruire sans discrimination de sexe ou de classe sociale. Gratitude aussi envers tous ceux qui m'ont accompagnée et soutenue toutes ces années.

Je remercie sincèrement mes directeurs, Pierre Magnan et David Marcogliese d'avoir cru et investi en moi. Grâce à leur soutien, j'ai pu bénéficier d'un milieu qui offre une facilité de recherche et où la curiosité, le dynamisme et les connaissances des collègues rendent l'apprentissage agréable et stimulant. Je remercie Andrée Gendron pour son aide et son attention lors de mes visites au Centre Saint-Laurent ainsi qu'à Pierre Gagnon pour son aide à réaliser certaines analyses statistiques. Un gros merci à Andrée-Anne Beaudoin, Dave Gadbois Côté, et Gabriel Pepin, qui ont pendant des dizaines d'heures consciencieusement, patiemment, extrait et compté des parasites. Merci également à toutes les autres personnes qui ont participé au projet : Marie-Ève Deshaies, Maxime Léveillé, François Darchambeau, Marianne Théberge, Andrea Bertolo, Rémi Bacon Émélie Mercier, Christian Desgagné.

Je tiens à remercier Philippe Brodeur et Marc Mingelbier, toujours volontaires pour échanger des informations et des idées, ainsi que Claude Lemire, tout aussi généreux et ouvert aux échanges.

Et vous, qui étiez au départ mes collègues et qui êtes devenus mes amis : Angélique Dupuch, Andrea Bertolo, Véronique Boily, Chantal Fournier, Marc Pepino, Marianne Théberge. Merci de votre présence et de votre écoute.

Merci mes enfants, Louis, Romi, Daphné, qui m'avez vue, trop souvent, m'isoler pour travailler. Merci à vous qui avez eu à apprendre à vivre avec des revenus

minimaux, mes revenus d'étudiante n'étant jamais bien élevés. Merci Salomé et Julie de faire partie de ma vie.

Je réserve le mot de la fin à Gilbert Cabana, mon compagnon de vie, pour son soutien sans limites. Merci Gilbert, d'être à mes côtés.

Je dédie cette thèse à toutes celles et ceux qui n'ont pas la chance de s'instruire.

Comme les grenouilles après un long hiver, puisse l'humanité

sortir de sa torpeur et chanter, enfin, l'hymne au printemps

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RÉSUMÉ

Afin de compenser pour la perte de ses milieux humides due aux activités anthropiques, de nombreux marais ont été aménagés de long des rives du fleuve Saint-Laurent. Seize d'entre eux sont localisés dans la plaine inondable du lac Saint-Pierre, dernier élargissement du fleuve. Le lac Saint-Pierre occupe une superficie d'environ 350 km^2 et une profondeur moyenne d'environ trois mètres, excepté au centre, dans le chenal de navigation, où la profondeur est d'environ 11 mètres. Le lac est formé de masses d'eau ayant des caractéristiques physiques et chimiques bien distinctes et qui coulent côte à côte, se mélangeant peu. Le lac Saint-Pierre est le lieu d'une importante pêcherie. La perchaude, *Perca flavescens*, y a occupé une place majeure pendant plus d'un siècle autant au niveau de la pêche commerciale que sportive. Toutefois, à la suite du déclin de la densité de la population, des mesures destinées à limiter son exploitation furent mises en place. Malgré les efforts déployés, la question à savoir si la population de perchaudes devrait être considérée comme étant constituée d'un ou plusieurs stocks demeure toujours. La délimitation des stocks est fondamentale en gestion des ressources. Ne pas tenir compte de la structure des stocks peut avoir des impacts considérables sur les caractéristiques biologiques et la productivité d'une population. Une saine gestion des pêches requiert une approche holistique qui exige l'acquisition de connaissance, notamment, sur la structure spatiale et les déplacements des individus. L'échelle spatiale à laquelle les activités d'alimentation d'un consommateur se déroulent est d'un intérêt fondamental puisqu'elle détermine l'échelle spatiale des interactions prédateurs-proies. Les parasites ainsi que les isotopes stables du carbone et de l'azote sont des marqueurs qui fournissent de l'information à la fois sur les patrons spatiaux et les réseaux trophiques dont font partie les individus. Nous avons profité des qualités de ces marqueurs pour tester un certain nombre d'hypothèses reliées à la biologie, notamment les patrons spatiaux, de la perchaude du lac Saint-Pierre. Cette espèce, dont l'aire de distribution couvre une bonne partie de l'Amérique du Nord, est abondante et prisée par les pêcheurs commerciaux et sportifs. Elle occupe de plus une place d'importance à l'intérieur de nombreux réseaux trophiques. Compte tenu de l'importance qu'occupent les marais aménagés en tant qu'habitats de fraye et d'alevinage pour la perchaude et pour plusieurs autres espèces de poisson, nous nous sommes intéressés à leur réseau trophique. Les marais aménagés se distinguent des marais naturels du lac Saint-Pierre par une absence de fluctuation des niveaux d'eau et par une connectivité réduite. La diversité et la richesse spécifique des parasites de perchaudes juvéniles étaient moins élevées dans les marais aménagés que dans les marais naturels. De plus, les glochidies et les parasites dont le cycle de vie implique des bivalves étaient absents des marais aménagés, suggérant qu'une réduction des variations naturelles des niveaux d'eau, combinée à une connectivité réduite, peut avoir un impact sur certaines composantes du réseau trophique. Par ailleurs, la structure spatiale de la population de perchaudes du lac

Saint-Pierre est mal connue. Alors qu'aucune différence génétique n'a été observée entre des perchaudes provenant de différents secteurs du lac, d'autres études suggèrent que la population est structurée spatialement. Nous avons utilisé les parasites ainsi que les isotopes stables du carbone ($\delta^{13}C$) pour déterminer si la population de perchaudes du lac Saint-Pierre est constituée d'un ou plusieurs stocks. Les parasites ont permis de distinguer quatre stocks et le $\delta^{13}C$ en a différentié un cinquième. De plus, autant les parasites que le $\delta^{13}C$ ont révélé que les perchaudes âgées de cinq semaines étaient, elles aussi, structurées spatialement. Nos résultats suggèrent qu'au lac Saint-Pierre la population de perchaudes est constituée de différents stocks qui demeurent distincts au moins jusqu'à ce que les individus aient atteint leur troisième année. Le $\delta^{13}C$ nous a également permis d'estimer l'étendue de l'habitat d'alimentation des perchaudes du lac Saint-Pierre. Grâce aux valeurs contrastantes du $\delta^{13}C$ du carbone inorganique dissous entre la masse d'eau centrale et celles qui coulent de part et d'autre, nous avons développé un modèle simple mettant en relation le $\delta^{13}C$ d'invertébrés peu mobiles et leur distance de la rive et du chenal de navigation. Le $\delta^{13}C$ des invertébrés variait suivant le gradient rive-chenal, avec des valeurs plus négatives près de la rive et moins négatives près du chenal. La comparaison de la variabilité du $\delta^{13}C$ des perchaudes et celle des consommateurs primaires a permis d'estimer que sur l'axe rive-chenal, l'étendue de l'habitat d'alimentation des perchaudes adultes était d'environ 3 km et que cette étendue n'était pas influencée par leur âge. Par ailleurs, le $\delta^{15}N$ et les parasites indiquaient qu'il n'y avait pas d'augmentation de position trophique et qu'il n'y avait pas de changement de régime alimentaire chez les perchaudes 1+ à 3+. Ces résultats suggèrent que l'étendue de l'habitat d'alimentation d'un individu pourrait être plus influencée par sa position trophique que par sa taille. Nos résultats indiquent qu'individuellement, les perchaudes du lac Saint-Pierre s'alimentent à l'intérieur d'un territoire relativement restreint, mais que l'ensemble de la population se distribue à l'intérieur d'une bonne partie du lac.

Mots clés : plaine inondable, marais, connectivité, hydrologie, diversité, stock, marqueur biologique, parasite, isotope stable, réseau trophique, gradient spatial, habitat d'alimentation

INTRODUCTION GÉNÉRALE

Source de nourriture et d'eau douce, routes naturelles pour le commerce et les déplacements, les grandes rivières ont joué un rôle majeur dans la fondation de plusieurs grandes villes. Elles ont, toutefois, été aussi perçues comme un moyen pratique d'élimination des rejets municipaux, agricoles ou industriels (Corcoran *et al.* 2010). De nombreuses collectivités se sont historiquement établies dans les plaines d'inondation, profitant ainsi d'une terre riche en nutriments. Afin de réduire les menaces d'inondation et les dommages qu'elles accompagnent, des mesures d'atténuation ont souvent été mises en place, telles que la construction de structures de protection ou de régulation des niveaux d'eau. C'est ainsi que la majorité des grandes rivières sont soumises à de fortes pressions anthropiques étant fréquement aménagées ou contrôlées de façon à satisfaire les besoins des activités humaines ou encore étant le lieu d'importantes pêcheries (Welcomme 2008).

Il est de plus en plus reconnu qu'une saine gestion de la ressource requiert une approche holistique exigeant l'acquisition de connaissances sur les habitats et la biologie, incluant la structure spatiale et les déplacements, des espèces cibles et non cibles (Botsford *et al.* 1997, Francis *et al.* 2007, Wakeford *et al.* 2009). L'échelle spatiale à laquelle les activités d'alimentation d'un consommateur se déroulent est d'un intérêt fondamental autant dans un contexte de gestion que d'un point de vue écologique puisqu'elle détermine l'échelle spatiale des interactions prédateurs-proies. Par exemple, McCann *et al.* (2005) ont démontré à l'aide de modèles simples que les consommateurs qui occupent des positions trophiques élevées couplent les réseaux trophiques dans l'espace. Toutefois, l'échelle spatiale à laquelle ces interactions se déroulent ainsi que les possibilités d'expansion de l'espace exploité ont un effet déterminant sur la dynamique et la stabilité des réseaux trophiques (McCann *et al.* 2005).

Vu leur dynamisme, les patrons spatiaux peuvent être, d'un point de vue pratique, difficile à détecter, la pertinence des résultats dépendant souvent du marqueur utilisé pour réaliser une étude. L'avantage des marqueurs biologiques, comparativement aux marqueurs extrinsèques, est qu'ils fournissent de l'information à la fois sur les patrons spatiaux des individus et sur d'autres aspects de leur biologie. Les parasites sont particulièrement intéressants à cet égard. Étant dépendant de la distribution de tous les hôtes impliqués dans leur cycle de vie, leur présence dans un hôte indique que les autres hôtes sont présents dans l'environnement. Ainsi, non seulement les parasites fournissent de l'information sur la présence d'autres membres de la communauté, mais ils reflètent les variations spatiales des facteurs qui favorisent la présence et l'abondance de ces hôtes. Pour cette raison, les parasites sont utilisés depuis plus d'un siècle pour identifier les stocks de poisson (revu dans Arthur 1997, MacKenzie et Abaunza 1998). De plus, grâce au lien étroit qui existe entre les parasites et leurs hôtes, ceux transmis par l'alimentation permettent d'identifier les interactions trophiques entre les organismes (revu dans Marcogliese et Cone 1997, Marcogliese 2003).

Les isotopes stables, notamment ceux du carbone et de l'azote, sont également de bons traceurs des patrons spatiaux et des relations trophiques (ex. Cabana et Rasmussen 1996, Vander Zanden et Vadeboncoeur 2002, Guelinckx *et al.* 2006, Rasmussen *et al.* 2009). Lors des activités photosynthétiques, dans le cas du carbone, ou d'assimilation, dans le cas de l'azote, un fractionnement des isotopes ^{13}C et ^{12}C, et ^{15}N et ^{14}N, naturellement présents dans l'environnement, a lieu chez les producteurs primaires. Ce fractionnement, exprimé sous la forme d'un rapport, soit $^{13}C/^{12}C$ ($\delta^{13}C$) et $^{15}N/^{14}N$ ($\delta^{15}N$), est fixé dans les tissus des producteurs primaires puis transmis aux consommateurs. Il y a par la suite, lors de la respiration dans le cas du carbone, et lors de l'assimilation, de la synthèse des protéines et de l'excrétion des produits azotés dans le cas de l'azote, un enrichissement de l'isotope lourd entre chaque niveau trophique. Cet enrichissement est d'environ 1‰ pour le carbone, et de 3-4‰ pour l'azote. En plus de la physiologie de l'organisme, les principaux facteurs qui influencent le $\delta^{13}C$ et le $\delta^{15}N$ des producteurs primaires aquatiques sont respectivement le $\delta^{13}C$ du carbone inorganique

dissous et l'importance de la couche limite, et le $\delta^{15}N$ de l'azote inorganique dissous et la concentration en azote. Puisque que ces facteurs varient localement, le $\delta^{13}C$ et le $\delta^{15}N$ des producteurs primaires à la base des réseaux trophiques affichent eux aussi des variations spatiales. Le signal isotopique étant transmis à l'ensemble du réseau trophique, le $\delta^{13}C$ et le $\delta^{15}N$ des organismes tracent à la fois des relations trophiques et les variations spatiales (Peterson et Fry 1987).

Problématique et objectifs de la thèse

Prenant sa source à l'embouchure du lac Ontario, le fleuve Saint-Laurent coule dans une région à haute densité de population et est soumis à de constantes pressions d'origine agricoles, urbaines et industrielles, particulièrement en amont de la ville de Québec (Gangbazo et Le Page 2005). Diverses structures, dont des barrages et des écluses, ont été construites pour la production hydro-électrique ou pour limiter l'inondation des propriétés riveraines. De plus, un chenal a été aménagé de façon à favoriser la navigation commerciale (Morin et Bouchard 2000).

Dernier élargissement majeur du fleuve Saint-Laurent, le lac Saint-Pierre a une superficie de près de 350 km^2 à niveau d'eau moyen et une profondeur moyenne d'environ 3 mètres, excepté dans le chenal de navigation où des dragages d'entretien sont effectués régulièrement de façon à maintenir une profondeur minimale de 11 mètres. En amont, un archipel d'une centaine d'îles abrite la plus grande héronnière d'Amérique du Nord (Centre Saint-Laurent 1991). Le lac est bordé par une importante plaine d'inondation d'environ 14 000 hectares (pour une crue récurrente aux deux ans), qui sert de point d'arrêt, au printemps, à des centaines de milliers d'oiseaux migrateurs. Le lac Saint-Pierre a été désigné site RAMSAR en vertu de la Convention relative aux terres humides d'importance nationale et Réserve mondiale de la biosphère par l'UNESCO. Plus de 167 espèces d'oiseaux nicheurs, 13 espèces d'amphibiens (Centre Saint-Laurent 1996) et 50 espèces de poisson (La Violette *et al.* 2003) y ont été recensées.

Le lac Saint-Pierre est formé de masses d'eau ayant des caractéristiques physiques et chimiques différentes, coulant côte à côte et ne se mélangeant que partiellement (Frenette *et al.* 2006, Hudon et Carignan 2008). Au centre se trouvent des eaux vertes minérales, en provenance des Grands Lacs. La masse d'eau qui coule au nord est formée principalement des eaux de la rivière des Outaouais auxquelles viennent s'ajouter celles de plus petits tributaires, notamment les rivières Maskinongé, du Loup et Yamachiche. Ces eaux brunes sont riches en nutriments, matière organique particulaire et carbone organique dissous. La masse d'eau au sud est un mélange des rivières Richelieu, Yamaska et Saint-François. Drainant des bassins versants à forte vocation agricole, ces rivières sont responsables d'une grande partie des contaminants d'origine agricole qui affectent le lac. Les eaux brunes du sud ont une concentration plus faible de matière organique particulaire que celles du nord. Elles sont toutefois riches en nutriments, en chl *a*, et en carbone organique dissous (Gangbazo et Le Page 2005, Frenette *et al.* 2006, Vis *et al.* 2007, Hudon et Carignan 2008).

La présence du chenal de navigation canalise une portion importante de l'écoulement. En effet, la masse d'eau centrale représente la plus large proportion (70%) du débit total annuel et le plus grand volume d'eau (Vis *et al.* 2007). Les flots rapides du centre, où le temps de résidence n'excède pas 0.5 jour, contrastent avec les flots lents près des rives, là où le temps de résidence peut atteindre plus de 120 jours, tout particulièrement en été lorsque les bancs de macrophytes sont bien développés (Hudon et Carignan 2008). L'influence de la rivière des Outaouais combinée à celle des plus petits tributaires fait en sorte que les fluctuations saisonnières des niveaux d'eau sont importantes, pouvant varier de plus de deux mètres. Par ailleurs, les variations interannuelles du niveau d'eau moyen peuvent, elles aussi, atteindre deux mètres (Environnement Canada, Archived Hydrometric Data).

Les interventions humaines sur le Saint-Laurent ont eu des conséquences majeures sur sa plaine inondable, se soldant par la disparition d'une surface importante des terres humides (Centre Saint-Laurent 1991). Afin de compenser pour ces pertes, un bon nombre d'aménagements fauniques furent installés à partir de 1976 le long de ses

rives, tout d'abord dans le contexte du Plan nord-américain de la gestion de la sauvagine (PNAGS) puis près d'une vingtaine d'années plus tard, suite à la création du Fonds de restauration de l'habitat du poisson (FRHAP) (Lepage et Lalumière 2003). Seize de ces aménagements gérés à la fois par des organismes gouvernementaux et privés furent développés dans la plaine inondable du lac Saint-Pierre (Mingelbier et Douguet 1999). Étant initialement conçus dans une perspective visant à favoriser l'habitat de reproduction de la sauvagine, on érigea des digues et des barrages autour de certains d'entre eux de façon à maintenir le niveau d'eau stable (Lepage et Lalumière 2003). On s'aperçut alors, de façon inattendue, que ces marais aménagés étaient utilisés par un grand nombre d'espèces de poisson comme site de fraye, d'alevinage et d'alimentation (Brodeur *et al.* 2004). En effet, leur faible profondeur, le réchauffement rapide de l'eau au printemps, la végétation dense et l'absence de courant en font des milieux recherchés autant par les espèces à reproduction hâtive que tardive (Lepage et Lalumière 2003). Toutefois, la réduction de l'importance des fluctuations du niveau d'eau dans ces marais a eu pour effet de perturber la dynamique naturelle de la végétation, tout en favorisant leur eutrophisation lorsque situés dans des secteurs agricoles, remettant en question leur mode de gestion actuel (Lepage et Lalumière 2003, Kaminski *et al.* 2006, Foucrier *et al.* 2007, O'Neal *et al.* 2008).

Avec sa densité et sa diversité élevées de poisson, le lac Saint-Pierre est le lieu d'une importante pêcherie depuis plus d'un siècle (Morneau 2000). La perchaude y occupe une place majeure autant d'un point de vue écologique, vu son abondance (Guénette *et al.* 1994), que social et économique, compte tenu de l'intérêt des pêcheurs sportifs et commerciaux pour cette espèce. Elle fut l'objet d'une exploitation particulièrement intensive à partir du début des années 1980 (Guénette *et al.* 1994). Toutefois, à la suite d'un déclin important de la densité de sa population, des mesures limitant son exploitation furent mises en place dès 1997, celles-ci devenant progressivement plus restrictives de façon à assurer la conservation de la population (Magnan *et al.* 2008).

Bien que des efforts considérables aient été déployés afin d'en limiter son exploitation, la question à savoir si la population de perchaude du lac Saint-Pierre devrait être considérée comme étant constituée d'un ou plusieurs stocks demeure toujours. La délimitation des stocks est fondamentale en gestion des ressources. Les mécanismes compensatoires qui stabilisent la structure démographique d'une population peuvent avoir lieu de façon indépendante entre les différents groupes dont est formée cette population (Waldman 1999). Ainsi, ne pas tenir compte de la structure spatiale d'une population peut conduire à la surexploitation de certains groupes et, subséquemment, avoir un impact considérable sur l'ensemble d'une population (Begg *et al.* 1999). Il importe ici d'ouvrir une parenthèse et de définir le terme « stock » qui réfère à un concept directement relié à la gestion des ressources. Il semble ne pas y avoir de consensus sur la définition et d'autres termes faisant référence à un niveau d'organisation comparable, soit en dessous de l'espèce, sont également utilisés : dème, unité de gestion, sous-population, contingent (Dizon *et al.* 1992, Booke 1999, Secor 1999). Secor (1999) suggère toutefois que tout niveau d'agrégation basé sur des comportements divergents de migration ou de l'utilisation de l'habitat à l'intérieur d'une population doit être considéré comme étant une unité de gestion, c'est-à-dire un stock. La prémisse de base généralement acceptée est que la variation du marqueur utilisé pour définir cette unité doit être plus grande entre les groupes examinés qu'à l'intérieur de chaque groupe (Booke 1999, Waldman 1999). Il est de plus reconnu qu'une discrimination des stocks en fonction de l'isolement reproducteur des populations cause un problème compte tenu de la fragilité des barrières reproductrices (Dizon *et al.* 1992). D'autre part, Waldman (1999) souligne l'importance d'un point de vue fondamental de reconnaître les stocks puisque, la différentiation se déroulant au niveau de l'espèce, le processus en est un de micro évolution. Ainsi, la discrimination des stocks est à la jonction de l'évolution et de la biologie (Waldman 1999).

C'est dans un contexte d'acquisitions de connaissances fondamentales sur un consommateur aquatique, soit la perchaude, et dans une perspective de gestion et conservation de la ressource que s'inscrit mon doctorat. La perchaude, dont l'aire de

distribution couvre une bonne partie du Canada et du Nord des États-Unis, est une espèce abondante et prisée autant au niveau de la pêche commerciale que sportive (Scott et Crossman 1974, Magnan 2002, Clapp et Dettmers 2004, Glover *et al.* 2008). De plus, jouant un rôle important dans le transfert d'énergie (Thorpe 1977), elle occupe une place majeure à l'intérieur de nombreux réseaux trophiques (Evans 1986, Fullhart *et al.* 2002).

Compte tenu de l'importance qu'occupent les marais aménagés en tant qu'habitats de fraye et d'alevinage pour la perchaude et pour de nombreuses autres espèces de poissons, nous nous sommes intéressés, au chapitre I, à leur réseau trophique. En effet, des questionnements concernant les effets d'une gestion qui omet de reproduire les fluctuations naturelles des niveaux d'eau dans les marais aménagés se posent de plus en plus. Dans le cadre du PNAGS, auquel participe le Canada, les États-Unis et le Mexique, et à la suite de l'application de politiques visant à protéger les milieux humides, de nombreux projets de restauration et d'aménagement de marais ont été mis en place en Amérique du Nord, particulièrement depuis la dernière décennie. On commence toutefois à observer des différences de réponses de la part des communautés biologiques entre les marais soumis à des variations hydrologiques et ceux dont le niveau d'eau est maintenu stable, les premiers affichant par exemple une plus grande abondance et diversité de la sauvagine et d'oiseaux aquatiques (Kaminski *et al.* 2006, O'Neal *et al.* 2008).

En contribuant à créer des habitats variés, les fluctuations spatiales et temporelles des niveaux d'eau favorisent la diversité des espèces (Murkin *et al.* 1997, Brock *et al.* 1999). En conséquence, la diversité pourrait être réduite dans les marais aménagés où le niveau d'eau est maintenu stable. De plus, les barrages et les digues érigées autour des marais réduisent la connectivité entre les marais aménagés et le fleuve. Les échanges continus de nutriments et d'organismes entre les milieux humides et le plan d'eau adjacent étant un facteur contribuant à favoriser la diversité des milieux humides (Mitsch et Gosselink 2000), la connectivité réduite des marais aménagés pourrait résulter en une faible diversité d'espèces comparativement aux marais naturels du lac Saint-Pierre. Le principal objectif du chapitre I a donc été d'examiner l'effet de la

réduction de la fluctuation des niveaux d'eau et de la connectivité sur les parasites des poissons vivant dans des marais aménagés. Considérant la relation qui existe entre la diversité des parasites et celle des hôtes impliqués dans leur cycle de vie (Simková *et al.* 2003, Hechinger et Lafferty 2005, Hechinger *et al.* 2007), nous avons émis l'hypothèse que la diversité de parasites serait moins élevée dans les marais aménagés où le niveau d'eau est maintenu stable que dans les marais naturels. Nous avons comparé les parasites des perchaudes juvéniles provenant de deux marais aménagés où le niveau d'eau est maintenu stable et où la connectivité avec le lac est réduite, avec les parasites des perchaudes juvéniles provenant de deux marais naturels du lac Saint-Pierre. Puisque les perchaudes juvéniles sont nées et ont toujours vécu dans les marais aménagés, nous étions ainsi assurés que le signal parasitaire observé serait caractéristique de ces marais. Les objectifs spécifiques du chapitre I étaient de (i) caractériser les parasites des perchaudes juvéniles provenant des deux types de marais, (ii) établir la similarité de la composition de la communauté de parasites entre les deux types de marais, et (iii) tester l'hypothèse que la diversité des parasites des perchaudes juvéniles sera plus élevée dans les marais naturels que dans les marais aménagés.

Le principal objectif du chapitre II était de déterminer si la population de perchaudes du lac Saint-Pierre est formée d'un ou plusieurs stocks à l'aide des parasites et des isotopes stables du carbone. Alors qu'une étude suggère qu'il n'y a pas de distinction génétique entre les individus provenant de différents secteurs du lac (Leclerc *et al.* 2008), d'autres études ont observé des différences de taille, de taux de croissance, et du rapport ARN/ADN entre les individus des rives nord et sud (Guénette *et al.* 1994, Tardif *et al.* 2005, Glemet et Rodriguez 2007), suggérant une certaine structure spatiale au sein de la population. Nous avons profité de l'hétérogénéité spatiale caractéristique du lac Saint-Pierre pour émettre l'hypothèse que si la transmission des parasites ainsi que le $\delta^{13}C$ à la base du réseau trophique varient localement, et si la population de perchaude est formée de différents stocks, alors les parasites et le $\delta^{13}C$ varieront entre les stocks. D'un autre côté, si la population est constituée d'un seul stock, aucune différence

de parasite et de $\delta^{13}C$ ne sera observée au sein de la population. Les données parasitologiques sont présentées à l'annexe du chapitre II.

Par ailleurs, alors que certaines études considèrent que la perchaude est une espèce sédentaire (Aalto et Newsome 1989, Hodgson *et al.* 1998), d'autres rapportent des déplacements importants (de Lafontaine *et al.* 2006, Glover *et al.* 2008). Lors d'une étude de marquage et recapture, Dumont (1996) a observé une fidélité au site mais aussi des déplacements de plus de 100 km chez les perchaudes du lac Saint-Louis, un autre lac fluvial du Saint-Laurent. Compte tenu de l'importance des échelles spatiales auxquelles se déroulent les activités des consommateurs sur le dynamisme des réseaux trophiques, l'objectif du troisième chapitre était de définir l'étendue de l'habitat d'alimentation de la perchaude du lac Saint-Pierre. Des études antérieures réalisées sur l'ensemble du Saint-Laurent (Yang *et al.* 1996, Barth et Veizer 1999) ont révélé que le $\delta^{13}C$ du carbone inorganique dissous ($\delta^{13}C_{DIC}$) différait entre les eaux en provenance des Grands Lacs et celles des tributaires. Nous avons donc émis l'hypothèse qu'un gradient spatial du $\delta^{13}C_{DIC}$ sera présent au lac Saint-Pierre le long de l'axe rive-chenal et qu'il sera possible, grâce à ce gradient, d'obtenir de l'information sur la position spatiale des perchaudes. Les objectifs spécifiques du chapitre III étaient de (i) établir si le $\delta^{13}C$ des consommateurs primaires suit un gradient le long de l'axe rive-chenal, (ii) déterminer la relation entre le $\delta^{13}C$ des consommateurs primaires et celui des prédateurs peu mobiles, (iii) déterminer l'étendue de l'habitat d'alimentation des perchaudes adultes en comparant la variabilité de leur $\delta^{13}C$ et celle du $\delta^{13}C$ des consommateurs primaires. Les valeurs de $\delta^{13}C$ des consommateurs primaires et des prédateurs peu mobiles sont présentées à l'annexe 1.

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CHAPITRE I

EFFETS DE L'AMÉNAGEMENT DES MARAIS SUR LES PARASITES DE PERCHAUDES JUVÉNILES

EFFECT OF WETLAND ENHANCEMENT ON PARASITES OF JUVENILE YELLOW PERCH

Résumé

Afin de favoriser l'habitat de reproduction de la sauvagine, le niveau d'eau de nombreux marais aménagés est maintenu stable à l'aide de digues et de barrages. L'étude a pour but d'examiner l'effet de la réduction de la fluctuation des niveaux d'eau et de la connectivité sur les parasites des poissons vivant dans des marais où de telles structures ont été érigées. Nous avons comparé les parasites de perchaudes (*Perca flavescens*) juvéniles provenant de deux marais aménagés où le niveau d'eau est maintenu stable et où la connexion avec le chenal principal a lieu seulement durant les épisodes de haut niveau d'eau (marais aménagés) aux parasites de perchaudes juvéniles provenant de marais soumis aux fluctuations naturelles du niveau d'eau et dont la connexion avec le chenal principal est continue (marais naturels). La richesse spécifique des parasites ainsi que l'indice de diversité de Shannon étaient plus élevés dans les marais naturels que dans les marais aménagés. L'indice de similarité de Jaccard a révélé que la composition de la communauté de parasites était plus similaire à l'intérieur qu'entre les deux types de marais. Les glochidies et les parasites dont le cycle de vie incluait des bivalves étaient absents des deux marais aménagés. Notre étude suggère que, dans les marais aménagés, des facteurs locaux tels que la réduction de la fluctuation des niveaux d'eau et de la connectivité peuvent limiter l'établissement des bivalves et que l'installation de digues et de barrages peut avoir un impact sur certains éléments du réseau trophique.

Abstract

Impoundments and dams are frequently used in wetlands to stabilize water levels and maintain breeding habitat for waterfowl. The objective of the study was to examine the effect of reduced water level fluctuations and connectivity on fish parasitism in wetlands caused by the installation of such structures.. We compared parasites of juvenile yellow perch (*Perca flavescens*) from two enhanced wetlands where water level is regulated and where connection with the main channel occurs only during spring flood (enhanced wetlands) to parasites of juvenile perch living in seasonally flooded wetlands where connection with the main channel is continuous (natural wetlands). Parasite species richness and Shannon diversity index were higher in natural than in enhanced wetlands. Jaccard similarity index revealed a higher similarity in parasite assemblages within than between each type of wetlands. Glochidia and parasites that include clams in their life cycle were absent from the two enhanced wetlands. Our study suggested that local factors such as water level fluctuation and connectivity in enhanced wetlands may limit the establishment of bivalves and that the use of impoundments and dams in wetlands areas may have an impact on some components of the food web.

Keywords : bivalves, connectivity, food web, impoundment, species diversity, water level

Introduction

Numerous wetlands were created or restored worldwide in the 1970s to compensate for their extensive losses in the past (Zedler and Kercher 2005; Acreman et al. 2007). In Canada and the U.S. many new wetlands were created or some already existing wetlands were modified to improve habitat for waterbirds and were, accordingly, kept permanently flooded with the help of structures such as impoundments and dams (Mingelbier and Douguet 1999; Mitsch and Gosselink 2000; Connor and Gabor 2006). This type of management guarantees that water depths satisfy waterfowl needs. However, it limits water level fluctuations and connectivity with adjacent water bodies, two hydrological factors that influence biological communities. While spatial and temporal water level variation creates a mosaic of habitats that promote species diversity (Murkin et al. 1997; Brock et al. 1999), hydrological connectivity determines exchanges of nutrient or organic matter as well as living organisms among water bodies (Amoros and Bornette 2002). Enhanced wetlands may benefit waterfowl when water level conditions are unfavorable in natural wetlands (Weber and Haig 1996; Connor and Gabor 2006). However, the effect of maintaining artificial hydrological conditions on other animal species have not been clearly assessed, particularly on fish parasites.

Parasites are of major interest because they are indicators of the surrounding taxa and of trophic linkages among them (Marcogliese and Cone 1997; Marcogliese 2003). Many parasites have a complex life cycle involving more than one host. For instance, digenean trematodes typically have a molluscan first intermediate host and an invertebrate or vertebrate second intermediate host that is then ingested by the definitive host. The extent to which parasite life cycles are completed locally within a habitat, the parasite community of a host will be related to the presence and occurrence of the animals occurring in that ecosystem (Marcogliese and Cone 1997; Marcogliese 2003). Consequently, parasites may be considered indicators of vertebrate and invertebrate species diversity and provide information on the structure of the food web (Marcogliese and Cone 1997; Marcogliese 2004; Lafferty et al. 2006; Lafferty et al. 2008).

Lake St. Pierre (LSP), the third fluvial lake of the St. Lawrence River (SLR), Québec, Canada, is large (350 km^2) and shallow, with a floodplain of approximately 18,000 ha consisting of extensive areas of wetlands. It has been designated as a Ramsar site and a UNESCO Biosphere Reserve. The lake is an important migratory stopover and breeding area for waterbirds. In the 1980s, more than 15 wetlands were enhanced in the lake's floodplain to improve habitat quality for waterfowl. In some of them, water level is artificially increased and maintained stable. The objective of the present study was to examine the effect of modifying two main components of floodplain wetlands, namely water level fluctuations and connectivity, on fish parasites. We compared parasites of juvenile yellow perch living in wetlands where water level is maintained stable and where connection to the main channel occurs only during spring flood (hereafter referred to as enhanced wetlands) to parasites of juvenile yellow perch living in seasonally flooded wetlands and where connection to the main channel is continuous (hereafter referred to as natural wetlands). We hypothesized that the parasite community will be more similar within than between each type of wetland. In addition, compared to fluctuating water level conditions, plant diversity is reduced when water level is stabilized (Keddy and Reznicek 1986; Wilcox and Meeker 1991). This may results in depauperate invertebrate communities (Wilcox and Meeker 1992; Bazzanti et al. 2003), reducing opportunities for parasite transmission. Moreover, by modifying environmental conditions, damming can influence fish parasite diversity (Loot et al. 2007). We therefore hypothesized that parasite diversity will be higher in natural than in enhanced wetlands.

Methods

Study sites

Lake St. Pierre (46° N, 72° W; Quebec, Canada) averages ~3 m depth at mean discharge, except in the deep (> 11 m) navigation channel that bisects the lake longitudinally. Waters originating from Lake Ontario are predominant in terms of flow (~80% of discharge), but are restricted to the navigation channel flowing from west to

east. The rest of inflow comes from tributaries draining the SLR lowlands (Morin and Bouchard 2000).

We selected two natural and two enhanced wetlands in the floodplain of LSP to test our hypotheses (Fig. 1). Natural wetlands were located on the north shore of the lake, along the progressively deepening littoral margins of the Maskinongé Bay and the Yamachiche Bay sectors. The water flowing through Maskinongé Bay originates from the Ottawa River and the northwest tributaries while the one flowing through Yamachiche Bay is mainly formed by the Du Loup and Yamachiche rivers (Frenette et al. 2003; Frenette et al. 2006). LSP is subjected to high annual water level fluctuations (Fig. 2). As a result, water depth in littoral areas may reach up to 2 m during spring flood but drops to a few centimeters in summertime (personal observation). This contrasts with the two enhanced wetlands of Lavallière Bay and du Moine Island, located in the archipelago of LSP, in the upstream part of the lake (Fig. 1). Wetlands were naturally present in these sectors. However, since 1986 at Lavallière Bay and 1999 at du Moine Island, impoundments and dams that keep large areas permanently flooded (600 and 172 ha, respectively) were built to benefit waterfowl (Lepage and Lalumière 2003; Foucrier et al. 2007). In these wetlands, water level is controlled and maintained at 5.2 m (geodesic reference) (Mingelbier and Douguet 1999). In springtime, enhanced wetlands are filled by snowmelt and by water from the surrounding areas. The main water mass that flows through both enhanced wetlands during spring flood, when water level of the SLR exceeds the height of the dams, originates from the Richelieu River. Lavallière Bay is also under the influence of the Yamaska River; the contribution of this river to fill the wetland is related to the duration of the flood, and thus varies annually. In addition, small streams and man made channels constantly feed this large enhanced wetland (Frenette et al. 2003; Foucrier et al. 2007). In du Moine Island, water supplies after the spring flood comes mostly from ground water (P. Brodeur, Ministère des Ressources Naturelles et de la Faune, personal communication). Individually, waters that flow through each wetland are a mixture of river and stream sources, and relative contributions are related to seasonal and annual hydrological conditions (Foucrier et al.

2007; Vis et al. 2007). Rivers and streams feeding all four wetlands are impacted by agricultural activities of the SLR lowlands and thus periodically receive high nutrient and suspended particulate matter input (Foucrier et al. 2007; Hudon and Carignan 2008). As a result, physical and chemical constituents of each of the four wetlands exhibit high intra- and inter-annual variability.

The natural and enhanced wetlands are used by waterbirds as resting areas and by fishes, including yellow perch, for spawning in spring (Lepage and Lalumière 2003; Foucrier et al. 2007). High water levels in spring make the enhanced wetlands accessible to fish, which lay their eggs inside the wetlands. However, after flooding subsides, connectivity with the surrounding water bodies and the enhanced wetlands is disrupted. In du Moine Island, newly hatched fish and adult fish that did not leave the wetland after spawning are captured inside the impoundments. To limit winterkill, managers transfer annually as many fish as possible from inside to outside the wetland. In Lavallière Bay, fish can leave the wetland through the dam at all times because of the permanent water supply from the small streams. Despite managerial operations in du Moine Island or the possibility to leave in Lavallière Bay, some fish stay inside the wetlands all year (Lepage and Lalumière 2003; Foucrier et al. 2007; P. Brodeur, Ministère des Ressources Naturelles et de la Faune, personal communication).

Fish sampling

Spawners might come from any area of LSP or the SLR. Therefore, to obtain a parasitic signature characteristic of each wetland we chose to examine parasites of the juvenile yellow perch that hatched in the wetlands. In this system, perch spawn mostly during the two last weeks of April and eggs hatch around the second week of May (Tardif et al. 2005). In enhanced wetlands, juveniles assembled just behind the dam. In the two natural wetlands, schools of juveniles were found in about 70 cm depth. At a single location for each wetland, we sampled 135–171 juveniles in each wetland with a seine (14.0–40.5 mm) on 28 June and 04 July 2005, at du Moine Island and Lavallière

Bay, respectively, and on 30 June 2005 in Maskinongé Bay and Yamachiche Bay (Table 1). Fish were fixed and stored immediately after capture in 75% ethanol.

Parasite analysis

We examined all organs and tissues for parasites with a stereomicroscope except for the blood and nervous systems. All parasites found were counted, fixed in 75% ethanol, and identified to genus following standard procedures. Due to their low number, we were unable to identify three taxa of nematodes and classified them as sp. 1, 2, and 3. We estimated the mean abundance and prevalence of parasites. Mean abundance was defined as the mean number of parasites of a given taxon per host, infected and uninfected, while prevalence was the proportion of hosts in a population infected with a particular taxon of parasites, expressed as a percent (Bush et al. 1997).

Statistical analyses

For each site, we calculated prevalence of infection by at least one parasite individual of any taxon, prevalence and mean abundance of each parasite taxon, and mean abundance of parasites grouped according to the hosts involved in the parasites' life cycle. We estimated similarity in parasite composition among wetlands by calculating a Jaccard similarity index with mean abundances (J) (Krebs 1999). We examined species richness (S) and calculated a Shannon diversity index (H) to evaluate parasite diversity within sites. We used Hutcheson's t test to test for differences in the Shannon index among sites (Zar 1999). Correlations between 1) Jaccard similarity index and geographical distance among sites, 2) fish mean length as well as mean weight and Shannon diversity index, and 3) fish mean length as well as mean weight and prevalence of infection by at least one parasite individual of any taxon were determined with Spearman rank correlations. We tested for differences in prevalence with Fisher's exact tests and in mean abundances among sites with Fisher-Pitman's permutation tests (p-values were adjusted for multiplicity using the Bonferroni-Holm method). We chose the non parametric Spearman rank correlation and permutation tests because data were not normally distributed.

Results

Juvenile yellow perch total lengths and body masses differed significantly among the four study sites (ANOVA, $p < 0.05$). Fish from du Moine Island were the longest and heaviest, followed by those from Yamachiche Bay and Maskinongé Bay, and finally by fish from Lavallière Bay (Table 1). We found a total of 14 taxa of metazoan parasites in juvenile yellow perch (Table 2). The prevalence of infection was particularly low in Lavallière Bay where only 14% of fish were infected by at least one parasite individual of any taxon in contrast with 76% in Maskinongé Bay (Table 1). In Yamachiche Bay and du Moine Island, prevalence of infection was of 31 and 35%, respectively (Table 1). Only *Ichthyocotylurus* spp., *Azygia angusticauda*, and *Proteocephalus* spp. were common to the four wetlands (Table 2). We observed significant differences in mean abundance among sites for *Tylodelphys scheuringi* (Maskinongé Bay > du Moine Island > Yamachiche Bay > Lavallière Bay; Fisher-Pitman's permutation test, $p < 0.001$), *Proteocephalus* spp., (Maskinongé Bay = du Moine Island > Yamachiche Bay = Lavallière Bay; $p < 0.01$), *Crepidostomum cornutum* and *Bunodera sacculata* (Yamachiche Bay = Maskinongé Bay > du Moine Island = Lavallière Bay; $p < 0.01$), and glochidia (Maskinongé Bay > Yamachiche Bay > du Moine Island = Lavallière Bay; $p < 0.001$) (Table 2). We obtained similar results for these parasites when we analyzed prevalence (results not shown).

Parasite species richness (S) was higher in natural wetlands than in enhanced wetlands. Eleven taxa were found in each of the natural wetlands compared to four and five taxa in Lavallière Bay and du Moine Island enhanced wetlands, respectively (Table 2). Shannon diversity index (H) was higher in natural wetlands than in enhanced wetlands and was also higher in Lavallière Bay than in du Moine Island (Hutcheson's t tests, $p < 0.005$; Table 1). No significant correlation was found between either fish mean length or mean weight and Shannon diversity index or prevalence of infection (Spearman rank correlation, $p > 0.05$). The greatest similarities among sites were observed between the two natural wetlands (J = 0.82) followed by the two enhanced

wetlands (J = 0.50) (Table 3). We found no significant correlation between geographical distance among sites and Jaccard similarity index (Spearman rank correlation, $p > 0.05$).

When parasites were grouped according to life cycles and transmission patterns, we observed that glochidia and parasites that include clams in their life cycle (*Bunodera sacculata* and *Crepidostomum cornutum*) were absent from the two enhanced wetlands. The mean abundance of parasites that infect snails and birds was significantly different among each sites, being significantly higher at Maskinongé Bay, followed by du Moine Island and Yamachiche Bay, and then by Lavallière Bay (Fisher-Pitman's permutation test, $p < 0.001$ in all cases). We also observed significant differences of mean abundance of parasites transmitted by copepod intermediate hosts (Fisher-Pitman's permutation test, Maskinongé Bay = du Moine Island > Yamachiche Bay ($p < 0.001$) > Lavallière Bay ($p < 0.05$)) (Fig. 3).

Discussion

The parasite communities of juvenile yellow perch differed considerably between natural and enhanced wetlands, similarities being higher within than between each type. In addition to host attributes (diet, body size, age), two major determinants of the parasite community within a host population are the regional pool of parasites species and local factors that define the habitats and influence the distribution and abundance of potential hosts (Hartvigsen and Kennedy 1993; Poulin and Morand 1999; Simková et al. 2003). Geographical distance and habitat characteristics are therefore important factors that determine parasites' distinctiveness or similarity among localities in a host species (Valtonen et al. 1997; Marcogliese et al. 2001; Poulin 2007). Thus, if colonization by parasites is not limited by distance or by obstacles that restrain the movement of mobile hosts, similarity among parasite communities suggests a similarity of habitats and of the potential host communities (Aho and Kennedy 1987). The absence of relationship between fish length or weight and parasite diversity or prevalence in our study suggests that the differences in the parasite community between natural and enhanced wetlands were not related to the attributes of the fish hosts. Furthermore, we did not observe any

relationship between geographical distance and similarity. Yellow perch parasites could be dispersed by their highly mobile vertebrate hosts, i.e. birds and fish, and colonize both types of wetlands. The separation of the enhanced wetlands from the main river after spring flood is not a limitation to parasite dispersal by fish because, despite the annual flushing by managers, some fish entering for spawning remain in the wetland all year. Therefore, the similarities in parasites of juvenile perch within each type of wetland most likely resulted from some local factors that structure the habitats and define the host community.

Among the main characteristics that could have affected the biological communities and that are simultaneously similar within and different between the two types of wetlands are those related to water level fluctuations and to hydrological connectivity. In enhanced wetlands, because of the low water level fluctuations and of the short temporal connection with the SLR, substrate scouring by ice and by flow velocity is reduced compared to natural wetlands. This favors the establishment of few large perennial taxa and the development of a substrate essentially composed of rhizomes anchored in a mixture of decomposed organic matter, silt and clay (Foucrier et al. 2007). In addition, sediments transported into enhanced wetlands in spring during high flood may be trapped behind the dams (Tockner et al. 1999; Svendsen et al. 2009). These factors most likely had a determining effect on the quality of the substrate and on the prevailing environmental conditions. Consequently, the similarities in perch parasites within each type of wetlands may result, in part, from their respective specific hydrological conditions.

The absence in enhanced wetlands of *Bunodera sacculata* and *Crepidostomum cornutum*, two digeneans that use sphaerid clams as first intermediate host, and of glochidia, the larval stage of unionid clams were notable. Digeneans are sensitive to environmental stress because both their free-living stages and their molluscan intermediate host can be affected (Lafferty 1997). Eggs and free-larval stages of digeneans are known to be sensitive to chemical and physical characteristics of the habitats such as temperature, pH, light, water mineral content, and desiccation (Pietrock

and Marcogliese 2003). Furthermore, negative effects on digeneans have been shown in fish exposed to chemical pollution (Valtonen et al. 1997), acidification (Marcogliese and Cone 1996; Halmetoja et al. 2000), and eutrophication (Kesting and Zander 2000), presumably via effects on molluscan intermediate hosts. In a comparison of four lakes affected to different degrees by chemical pollution, Valtonen et al. (1997) observed that glochidia were absent from the most chemically polluted lake. Unionid freshwater mussels are among the first benthic invertebrates to disappear when habitat quality degrades (Bogan 2008). While we had no precise information on the chemical constituents of the different water sources that fed the wetlands, the absence of parasites transmitted by clams and of glochidia suggested that environmental conditions in the enhanced wetlands somehow were limiting to bivalves. Factors such as oxygen depletion following the decay of the dense vegetation combined with high sedimentation rates might have been limiting to unionid and sphaerid clams, two filter-feeders intolerant of low-oxygen concentrations and siltation (Popp and Hoagland 1995; Burlakova and Karatayev 2007).

Parasite diversity and species richness were higher in natural than in enhanced wetlands. A few recent studies related diversity in one host species to the parasite diversity in an upstream or downstream host. For instance, Hechinger and Lafferty (2005) observed a positive relationship between bird diversity and the diversity of trematodes in snail intermediate hosts living in two different habitats of a Californian salt marsh, while Hechinger et al. (2007) found a positive relationship between species richness of trematodes in snail first intermediate hosts and species richness of large benthic second intermediate hosts. In a study comparing digeneans of black-headed gulls living around different reservoirs, Simková et al. (2003) showed that intermediate hosts' diversity and parasite diversity in the birds were related and were mainly influenced by local characteristics of each site. It is possible that the low parasite diversity observed in juvenile perch of enhanced wetlands was related to yearly winterkill, limiting the establishment of a well developed and diverse invertebrate community (Smith et al. 2005) and thus of potential intermediate hosts. In addition, while the fish community is

composed of more than 50 fish species in LSP (La Violette et al. 2003), only 27 species were recorded in Lavallière Bay (Foucrier et al. 2007). Differences in fish community structure also may affect macroinvertebrate species composition through differential predation (Williams et al. 2003; Persson and Svensson 2006). Corti et al. (1997) observed that the structure of benthic invertebrate communities in floodplain ponds was strongly affected by hydroperiod. Invertebrate taxa richness, abundance, and biomass were lower in permanent than in periodically drying ponds, probably because of higher vertebrate predation in permanent ponds. Parasite transmission dynamics are dependant on the abundance and distribution of every host in a parasite's life cycle (Marcogliese et al. 1990; Smith 2007). Moreover, high density of hosts increases transmission rate and promotes high abundance or prevalence of parasites (Bustnes et al. 2000; Coyner et al. 2002; Loot et al. 2005). The higher parasite diversity in natural wetlands suggests a higher food web complexity therein compared to enhanced wetlands.

Differences in perch parasites between natural and enhanced wetlands in Lake St. Pierre suggest that fundamental ecological differences exist between the two types of habitats. The reduced species richness in enhanced wetlands implies that their food webs have been compromised compared to natural wetlands. While the actual cause of the differences is not clear, they may be due to isolation of wetlands from surrounding waters or increased siltation, both of which result from dam construction and altered hydrology. Management of wetlands ecosystems would benefit from better knowledge of biological interactions following modification of hydrology.

Acknowledgments

We thank A. Gendron (Environment Canada) for her help in parasitological procedures, P. Gagnon (Environment Canada) his help with statistical analyses, R. Bacon, M-E. Deshaies, F. Darchambeau and M. Théberge for their logistic support and assistance in the field, A-A. Beaudoin, D. Gadbois-Côté and G. Pepin for their help in dissecting the fish, and P. Brodeur (Ministère des Ressources naturelles et de la Faune) for his

comments on a first version of this paper. We also thank the editor and two anonymous reviewers who provided helpful comments on an earlier draft. This study was supported by grants, the Natural Sciences and Engineering Research Council of Canada and Canada Research Chairs program to PM. and research funds from the St. Lawrence Action Plan (Environment Canada) to DM.

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Table 1: Number (N) and metrics of juvenile yellow perch captured in two natural (Maskinongé Bay and Yamachiche Bay) and two enhanced wetlands (Lavallière Bay and du Moine Island), prevalence (%) of fish infected by at least one parasite individual of any taxa, number of parasite taxa (S) found within each wetland, and Shannon diversity index (H)*.

Site	N	Date of capture	Mean length (± S.D.) (mm)	Length range (mm)	Mean weight (± S.D.) (g)	Body mass range (g)	Prevalence (%)	S	H
Maskinongé Bay	171	30-06-05	24.76 (3.70)	17.36 – 38.78	0.125 (0.061)	0.012 – 0.372	76	11	0.656 [a]
Yamachiche Bay	169	30-06-05	27.79 (3.92)	17.36 – 37.78	0.187 (0.080)	0.036 – 0.455	31	11	0.654 [a]
Lavallière Bay	138	04-07-05	18.04 (4.95)	14.01 – 40.49	0.069 (0.078)	0.017 – 0.521	14	4	0.488 [b]
du Moine Island	125	28-06-05	31.92 (2.42)	26.53 – 38.06	0.244 (0.060)	0.118 – 0.426	35	5	0.273 [c]

*Indices with different letters are significantly different.

Table 2: Hosts, mean abundance (SD), and prevalence (%) of parasites found in juvenile yellow perch from two natural (Maskinongé Bay and Yamachiche Bay) and two enhanced (Lavallière Bay and du Moine Island) wetlands.

Definitive hosts	Intermediate Host		Maskinongé Bay n = 171	Yamachiche Bay n = 169	Lavallière Bay n = 138	du Moine Island n = 125
		Trematoda metacercariae				
Piscivorous bird	1st: snail 2nd: fish	*Ichthyocotylurus* spp.	0.07 (0.36) 5 %	<0.01 < 1 %	0.03 (0.24) 1 %	<0.01 < 1 %
		Apatemon spp.	0.01 (0.11) 1 %	0	0	0
		Posthodiplostomum spp.	<0.01 < 1 %	<0.01 < 1 %	0	0
		Apophallus brevis	0.03 (0.17) 3 %	0.01 (0.11) 1 %	0	0
		Tylodelphys scheuringi	0.57 (0.99) 34 %	0.03 (0.20) 2 %	0	0.11 (0.35) 10 %
		Trematoda				
Fish	1st: sphaerid clam 2nd: cladoceran	*Bunodera sacculata.*	0.07 (0.32) 5 %	0.10 (0.39) 7 %	0	0
	1st: sphaerid clam 2nd: mayfly	*Crepidostomum cornutum*	0.06 (0.28) 5 %	0.03 (0.17) 3 %	0	0
	Snail	*Azygia angusticauda*	0.09 (0.28) 9 %	0.04 (0.22) 3 %	0.09 (0.37) 6 %	0.02 (0.14) 2 %
		Cestoda				
	Copepod	*Proteocephalus* spp.	0.81 (1.43) 36 %	0.42 (1.31) 17 %	0.20 (1.80) 4 %	0.75 (1.65) 27 %
		Nematoda				
		sp. 1	0	0	0.04 (0.19) 4 %	0
		sp. 2	0	0	0	0.02 (0.14) 2 %
		sp. 3	0	<0.01 < 1 %	0	0
Single Host: Fish		Mollusca				
		Glochidia	1.14 (2.77) 32 %	0.18 (1.13) 4 %	0	0
		Annelida				
		Myzobdella lugubris	<0.01 < 1 %	<0.01 < 1 %	0	0

Table 3: Jaccard similarity index (J)* values between metazoan parasites in juvenile yellow perch from two natural (Maskinongé Bay and Yamachiche Bay) and two enhanced (Lavallière Bay and du Moine Island) wetlands (below the diagonal), and approximate distance between sites (above the diagonal).

	Similarity and distance (km) between sites			
	Maskinongé Bay	Yamachiche Bay	Lavallière Bay	du Moine Island
Maskinongé Bay	-	12	12	12
Yamachiche Bay	0.83	-	21	20
Lavallière Bay	0.25	0.25	-	3
du Moine Island	0.33	0.33	0.50	-

*Similarity ranges from 0 (no similar taxa) to 1(completely similar taxa).

Figure legends

Figure 1 : Location of natural wetlands (hatched areas) and enhanced wetlands (solid areas) in Lake St. Pierre, Québec, Canada. A) Maskinongé Bay, B) Yamachiche Bay, C) Lavallière Bay, and D) du Moine Island.

Figure 2 : Average (SD) of monthly mean water level for 1995–2005 in Lake Saint-Pierre at the Sorel Station. (Adapted from

http://www.wsc.ec.gc.ca/hydat/H2O/index_e.cfm?cname=HydromatD.cfm)

Figure 3 : Mean abundance (error bars = SD) of *Azygia* sp. (IH snail), Trematoda metacercariae (1st IH snail and DH bird), *Proteocephalus* spp. (IH copepod), *Bunodera sacculata*. & *Crepidostomum cornutum*. (1st IH sphaerid clam and 2nd IH arthropod), and glochidia, in fish from Maskinongé Bay (white area), Yamachiche Bay (dashed area), Lavallière Bay (black area) and du Moine Island (grey area). Groups with a mean abundance < 0.01 are not shown. Bars with different letters are significantly different (Fisher-Pitman's permutation tests, $p < 0.001$)

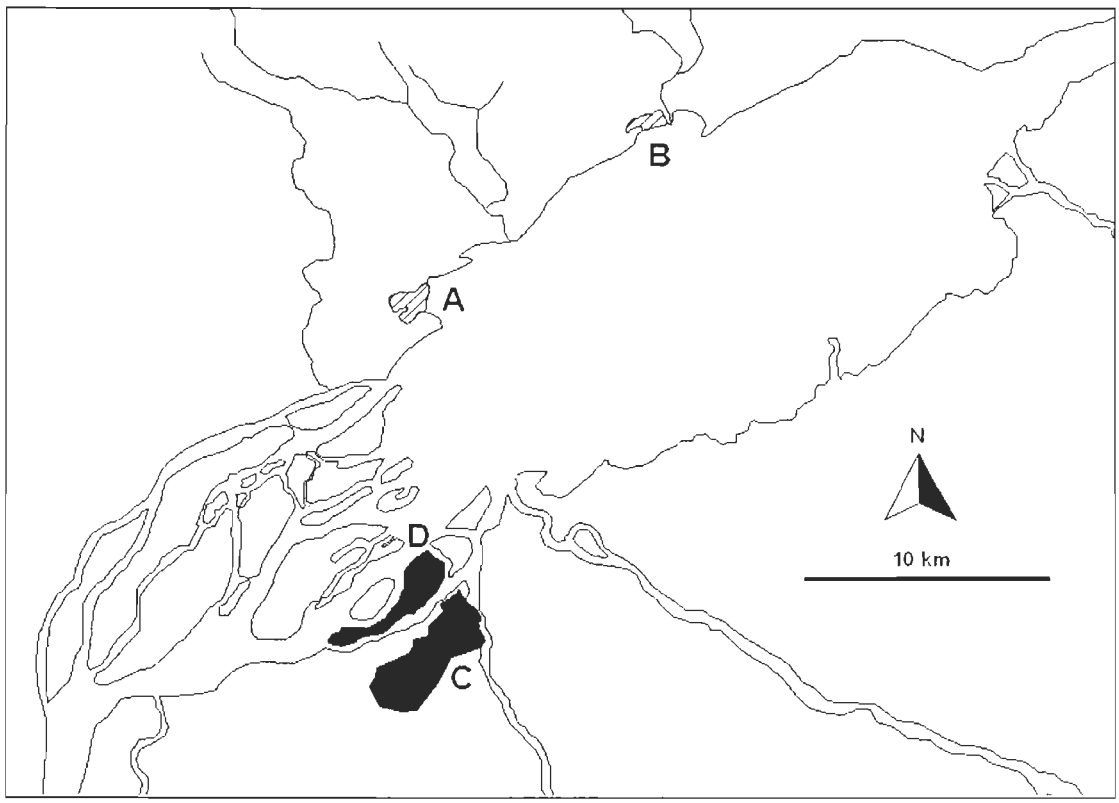

Figure 1

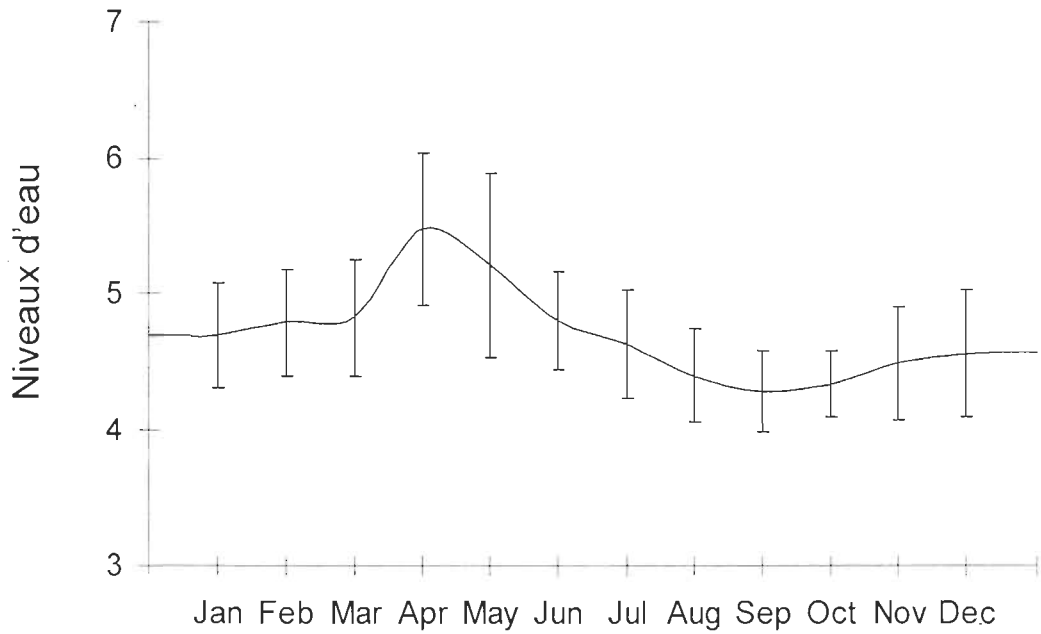
Niveaux d'eau
7
6
5
4
3
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec

Figure 2

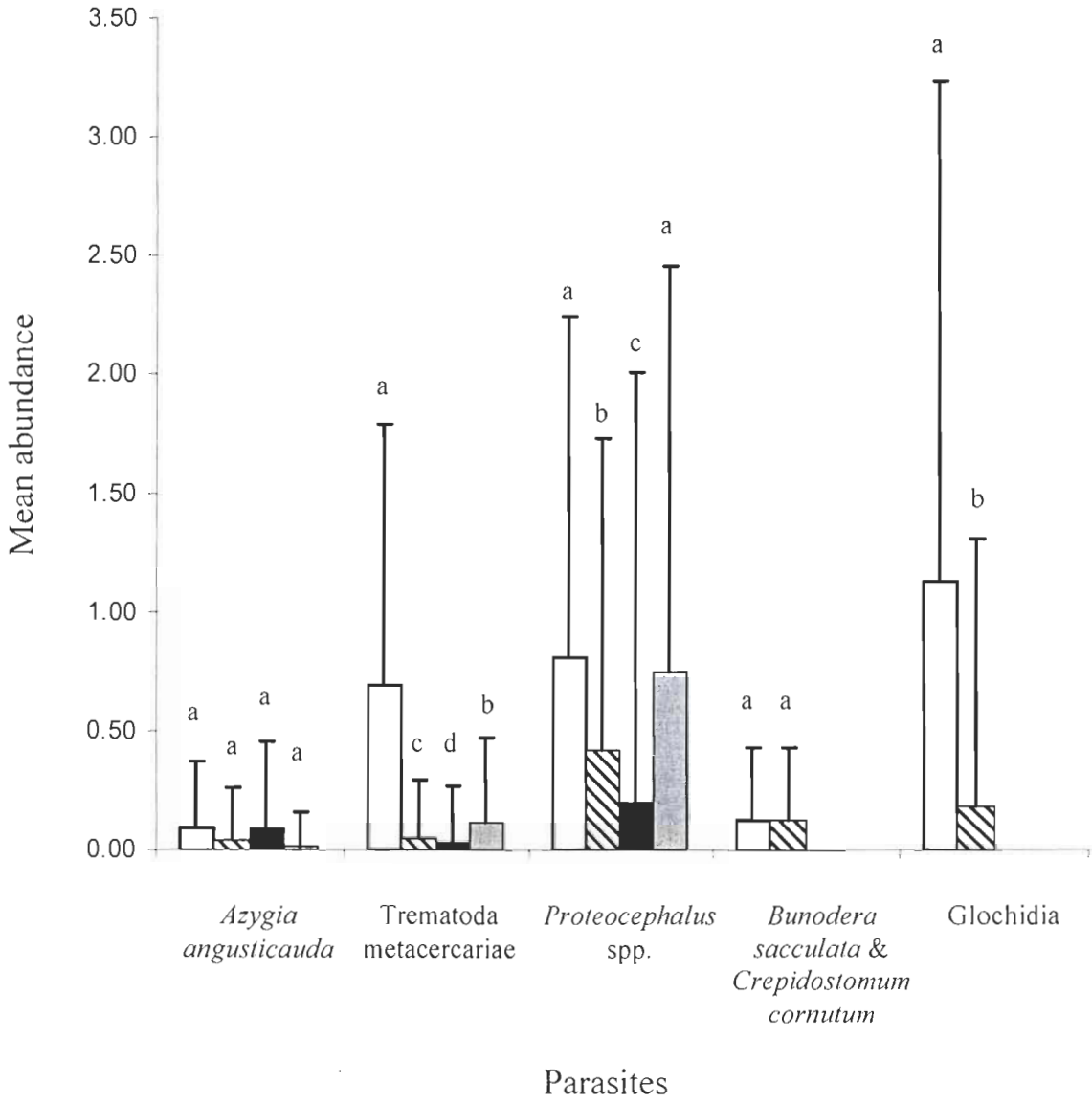
3.50
3.00
2.50
2.00
1.50
1.00
0.50
0.00
Mean abundance
a
a
a
a
c
d
b
a
b
c
a
a
a
a
b
Azygia angusticauda
Trematoda metacercariae
Proteocephalus spp.
Bunodera sacculata & *Crepidostomum cornutum*
Glochidia
Parasites

Figure 3

CHAPITRE II

IDENTIFICATION DE SOUS-POPULATIONS DE PERCHAUDES D'UN LAC FLUVIAL À L'AIDE DES PARASITES ET DES ISOTOPES STABLES DU CARBONE

IDENTIFICATION OF YELLOW PERCH SUBPOPULATIONS IN A LARGE FLUVIAL LAKE WITH THE USE OF PARASITES AND CARBON STABLE ISOTOPE RATIOS

Résumé

La structure spatiale de la population de perchaude du lac Saint-Pierre, un élargissement du fleuve Saint-Laurent (Québec, Canada), fut déterminée à l'aide des parasites et du ratio des isotopes stables du carbone. La population de perchaude du lac Saint-Pierre est en déclin et des mesures de conservation ont été récemment appliquées. Toutefois, la structure spatiale de la population reste encore mal connue. L'utilisation conjointe des deux techniques a permis de différencier cinq sous-populations. Les parasites ont distingué quatre sous-populations et les isotopes stables du carbone en ont différentié une cinquième. De plus, autant les parasites que le ratio isotopique du carbone ont révélé que les perchaudes âgées de cinq semaines étaient, elles aussi, structurées spatialement. Nos résultats suggèrent qu'au lac Saint-Pierre la population de perchaudes est constituée de différents stocks qui demeurent distincts au moins jusqu'à ce que les individus aient atteint leur troisième année. Notre étude démontre que l'utilisation de différentes techniques d'identification des stocks peut donner des résultats contrastants et souligne l'importance d'avoir recours à plus d'une approche lors de la mise en place de stratégies de conservation.

Abstract

The spatial structure of the yellow perch population of Lake St. Pierre, a fluvial lake of the St. Lawrence River (Quebec, Canada), was determine using parasites and carbon stable isotope ratios. The yellow perch population of Lake St. Pierre is in decline and conservation measures have been recently applied. However, whether or not this population is spatially structured remains unclear. Parasites distinguished four subpopulations and carbon isotope ratios showed an additional differentiation. When the two techniques were combined, five subpopulations were differentiated within the lake. Furthermore, both parasites and carbon isotopic ratios revealed that five week old fish were also spatially structured. These results suggest the existence of distinct subpopulations in Lake St. Pierre which remain differentiated up to at least the third year. Our study demonstrates that contrasting results may arise with different techniques of stock identification and emphasizes the importance of using more than a single approach when developing conservation and management strategies.

Keywords : biological tracer, stock, conservation, management, spatial structure

Introduction

After more than two decades of decline, many fisheries are still collapsing, suggesting that management strategies are not always adequate (Mullon et al. 2005; Branch 2008). To counter that threat, many fisheries scientists have called for enforcement of management practices that consider the spatial structure of fish populations (Pikitch et al. 2004; Sethi et al. 2005). Determining well-defined spatial units of exploited populations is of major importance as a population may look healthy even though some subpopulations are collapsing (Begg and Waldman 1999). Furthermore, any habitat enhancement or fishing regulation will be of little effect if processes regulating a fish management unit occur in areas other than those under management (Francis et al. 1996). Nevertheless, identification of subpopulations remains a major challenge and often results in contrasting outcomes among studies (Begg et al. 1999; Abaunza et al. 2008).

The use of parasites to distinguish stocks has gained increased recognition in fisheries management (Abaunza et al. 2008, Zischke et al. 2009, Luque et al. 2010). Because they are linked to the distribution of all hosts involved in their life cycles, their presence in fish varies with the spatial variation of their different hosts. Parasites have been largely used to distinguish marine fish stocks (reviewed in Arthur 1997, MacKenzie and Abaunza 1998) but, on a few occasions they also have been shown to be good markers of stock structure in freshwater ecosystems (Bowen and Stedman 1990; Balling and Pfeiffer 1997; Marcogliese et al. 2001b). Moreover, some studies showed that within a single lake, parasites can discriminate individuals of the same fish species which participate in planktonic or benthic food webs (Curtis et al. 1995; McCairns and Fox 2004; Bertrand et al. 2008). This suggests that parasites are good markers of spatial patterns occurring at fine spatial scales.

Stable carbon isotope ratios ($\delta^{13}C$) are increasingly used to provide information on habitat use by an organism (Gray et al. 2004; Cunjak et al. 2005; Quevedo et al. 2009). $\delta^{13}C$ of aquatic primary producers varies spatially as it is determined by locally

variable factors such as $\delta^{13}C$ of dissolved inorganic carbon and the thickness of the boundary layer (Osmond et al. 1981; Hecky and Hesslein 1995). It is further transmitted through the food web with a typically slight increase of 0-1‰ between a consumer and its prey (DeNiro and Epstein 1978). Thus, because $\delta^{13}C$ differs among individuals that live in habitats where the food webs are isotopically distinct, it permits the assessment of fish stock structure (Takai and Sakamoto 1999; Gao et al. 2005; Bergstad et al. 2008).

Yellow perch (*Perca flavescens*) is considered to be a relatively sedentary species exhibiting homing and site fidelity (Aalto and Newsome 1989; Hodgson et al. 1998). However, mark-recapture experiments report extensive movements (Dumont 1996; de Lafontaine et al. 2006; Glover et al. 2008), questioning the sedentary behaviour of this species. Besides, while a study examining the genetic structure of the yellow perch population of Lake St. Pierre, a fluvial lake of the St. Lawrence River, revealed no differentiation within the lake (Leclerc et al. 2008), differences in growth rates and size of individuals between the north and south shores have been observed (Guénette et al. 1994; Tardif et al. 2005), suggesting a spatially structured population.

The main objective of the present study was to determine if the yellow perch population of Lake St. Pierre (LSP) is spatially structured, based on parasites and carbon stable isotope ratios. Until recently, this population was the target of extensive commercial and recreational fisheries (Magnan 2002), but strong population density decline led to strict harvest regulations. LSP is highly heterogeneous in terms of physical, chemical, and biological characteristics (French and Petticrew 2006; Vis et al. 2007; Hudon and Carignan 2008). We took advantage of this heterogeneity and hypothesised that if parasite transmission and $\delta^{13}C$ of the resource vary locally, and if the perch population is partitioned into subpopulations, parasites and $\delta^{13}C$ of perch will differ among them. Alternatively, if the perch within the population are vagile, no distinct parasite assemblages and isotopic signatures will be observed.

Materials and methods

Study area

Lake St. Pierre (LSP), Québec, Canada, is large (350 km^2) and shallow (average depth at mean discharge approx. 3 m) except in the navigation channel (depth approx. 11 m) which separates the north and the south shores. Three main water masses that differ in DOC, phosphorus, Chl *a* concentrations and in their optical properties flow through the lake with very limited lateral mixing (Frenette et al. 2006; Hudon and Carignan 2008). Three sampling sites minimally 10 km apart were selected on each shore, that is Maskinongé (46°12'N, 72°59'W), Yamachiche (46°16'N, 72°51'W) and Rivière-aux-Glaises (46°17'N, 72°44'W) on the north, and Anse-du-Fort (46°07'N, 72°54'W), Longue-Pointe (46°08'N, 72°47'W) and Nicolet (46°11'N, 72°40'W) on the south (Fig. 1). Habitats of the south shore are not particularly affected by fetch from the southwest and are characterized by a slow water transit which may reach up to 120 days at the end of summer (Hudon and Carignan 2008). At the Longue-Pointe and Nicolet sampling locations, a wide littoral margin deepens progressively over a gentle slope where extensive macrophyte beds develop over large areas measuring square kilometres, while the littoral margin is slightly more abrupt at Anse-du-Fort. On the north shore, transit time never exceeded twenty days. The Yamachiche and Rivière-aux-Glaises sampling sites are exposed to wind and waves with steep slopes, which limits the extent of macrophytes. The Maskinongé site is more sheltered from winds and waves, and the topography is more similar to the Longue-Pointe and Nicolet sectors (Vis et al. 2007; Hudon and Carignan 2008).

Yellow perch sampling

Yellow perch were sampled on their spawning grounds, from 23 to 30 April 2004 and 18 April to 08 May 2005, from commercial fishers except at Rivière-aux-Glaises where no commercial fishing occurs. At this location, we captured perch with similar gear (fyke nets) and techniques to those used by commercial fishers. We also captured 0+ perch at Maskinongé and Yamachiche sites with a seine on 30 June 2005. Because only few centimetres of water remain in the floodplain areas after spring flood, our sampling locations for 0+ perch were shifted approximately one km toward the centre of

the lake. Fish were frozen at -4° C after capture. Fish weight (± 0,01 g) and length (± 1 mm) were measured after thawing. We determined perch age from annuli on operculum (Baker and McComish 1998). Fish length, age or sex could have an effect on the parasite fauna or $\delta^{13}C$. Therefore, we subsampled perch in order to have similar age groups and sex ratio at each site. With this selection, analyses among sites were performed on a minimum of 16 individuals at each site for each age group (Appendix).

Parasite analysis

We examined parasites on more 0+ individuals than for other groups because infection rate is generally extremely low at this age (Appendix). With the exception of blood and nervous system, all organs and tissues were examined for parasites with a dissecting microscope. To estimate their abundance and prevalence, all parasites encountered were removed, fixed in ethanol 75% and identified to species or genus (Schmidt 1970; Arai 1989; Gibson 1996; Hoffman 1999) following standard procedures, including staining and mounting. Mean abundance is defined as the total number of parasites of a given taxon in a group of fish divided by the number of fish examined, infected and uninfected, while prevalence is the proportion of fish in a population infected with a particular taxon of parasites, expressed as the percent of fish examined (Bush et al. 1997).

Because the different developmental larval stages of the nematode *Raphidascaris acus* are indicators of different transmission pathways, we distinguished larval stages L2 and L3 from L4 and adults, based on the parasite localization in the fish. Indeed perch can act both as intermediate or definitive host of this nematode (McDonald and Margolis 1995). In the former case, *R. acus* is found in the fish liver at the L2-L3 developmental larval stages, and in the latter case in the intestine at stage L4 and adults.

Isotopic analysis

For isotopic analyses, a piece of dorsal muscle was taken from the back of each fish, except for 0+ perch for which we used the whole body because of their small size. For this age group, isotopic analyses were made only on 17 (Maskinongé) and 16

(Yamachiche) individuals randomly selected among those that were parasitized by at least one parasite of any taxa. Fish samples were dried at 60° C for at least 48 hours, ground into a homogeneous powder, and sent for isotopic analysis at the University of New Brunswick where they were analysed with a Finnigan Delta Plus mass spectrometer. The accuracy of the mass spectrometer computed from duplicates of 28 samples was ≤ 0.2‰.

Statistical analyses

We used Canonical Variate Analysis (CVA), on Hellinger transformed data (Legendre and Gallagher 2001), to discriminate perch among sampling sites, based on their parasite abundance. The CVA was tested with Monte Carlo simulation based on 9999 unrestricted permutations. We retained only the parasite taxa that explained a significant proportion of the among-sites variation (at a significance level corrected for multiple comparisons; 0.05/18 taxa = 0.0003; Bonferroni procedure). To eliminate the possibility that observed similarities or differences resulted from inter-annual variations or from differences in fish age, we performed the analysis among sites within each age class and year. Results of the CVAs performed on 2+ and 3+ perch captured in 2005 were very similar. We therefore performed CVAs on the two age classes combined. Analysis of variance (ANOVA) followed by *post hoc* Bonferroni tests were used to compare perch $\delta^{13}C$ among sampling sites, among age classes, and between years within sites. Similarly to parasites, no significant differences of $\delta^{13}C$ were observed between 2+ and 3+ perch, both in 2004 and 2005. Analysis were thus performed on the two age classes combined.

All analysis were performed with CANOCO for Windows, version 4.5 (Ter Braak and Smilauer 2002) and with SAS (version 9.1, SAS Institute, Cary, North Carolina).

Results

Parasitological analysis

We identified 18 taxa of metazoan parasites in perch from Lake St. Pierre (Appendix). Significant discriminations of the sampling sites were observed for every age group ($p < 0.01$) and most of the variance was generally explained by the first two axis. For 2+-3+ perch captured in 2004, the first axis of the CVA discriminated Anse-du-Fort, Nicolet and Longue-Pointe from Maskinongé, while the second axis discriminated Anse-du-Fort and Maskinongé from Nicolet and Longue-Pointe (Fig. 2a, Table 1). Abundance of *Crepidostomum cornutum* was positively associated with Anse-du-Fort, *Echinorhynchus lateralis* with Maskinongé, and *Diplostomum* spp. with Nicolet and Longue-Pointe (Fig 2a). In 2005, CVA significantly discriminated 0+ perch captured at Maskinongé from those at Yamachiche, abundance of *Tylodelphys scheuringi, Proteocephalus* sp. and glochidia being positively associated with fish from Maskinongé (Table 1, Appendix). For 1+ perch collected in 2005, the first axis of the CVA discriminated Maskinongé from Yamachiche and Anse-du-Fort, and the second axis discriminated Maskinongé and Yamachiche from Anse-du-Fort (Fig 2b, Table 1). Abundance of *R. acus* (L2-L3) was associated with Anse-du-Fort, and *C. cornutum* with Yamachiche (Fig. 2b). For 2+-3+ perch captured in 2005, the first axis discriminated Nicolet and Longue-Pointe from Yamachiche, Rivière-aux-Glaises and Maskinongé, while the second axis discriminated Maskinongé from the four other sites (Fig. 2c, Table 1). Abundances of *T. scheuringi* and *Diplostomum* spp. were positively associated with Nicolet and Longue-Pointe, *E. lateralis* and *B. sacculata* with Maskinongé, and *C. cornutum* with Yamachiche and Rivière-aux-Glaises (Fig. 2c).

Isotopic analysis

$\delta^{13}C$ of perch was highly variable, ranging from -33.6 to -14.6 ‰ (Fig. 3). At Maskinongé and Yamachiche, $\delta^{13}C$ of 0+ perch was lower than other age classes (ANOVA, $p < 0.0001$, r^2: 0.35; Fig 3). Mean $\delta^{13}C$ of 0+ perch and of adults (1+, 2+, 3+ combined) was respectively -30.22 ‰ (S. D. = 0.55) and -22.28 ‰ (S. D.: 3.53) at Maskinongé, and -32.40 ‰ (S. D. = 1.15) and -22.24 (S. D.: 3.59) at Yamachiche. 0+ perch from Yamachiche had more negative $\delta^{13}C$ than those from Maskinongé (*t*-test, $p <$

0.0001, r^2: 0.63; Fig. 3). In 2005, $\delta^{13}C$ of 2+-3+ perch from Longue-Pointe was more negative than $\delta^{13}C$ of 2+-3+ perch from all other sites (ANOVA, $p < 0.0001$, r^2: 0.14; Fig. 3). Between years differences of $\delta^{13}C$ were observed in perch 2+-3+ from Longue-Pointe, these being more negative in 2005 than in 2004 (*t*-test, < 0.0001, r^2: 0.43; Fig 3).

Discussion

When parasites and $\delta^{13}C$ were combined, five subpopulations were differentiated in Lake St. Pierre. The use of the two techniques provided complementary information. Parasites distinguished four subpopulations while carbon isotope ratios showed an additional differentiation.

Comparisons among sites

Parasites suggested that yellow perch were spatially structured into four groups, formed on the north shore by fish from (1) Maskinongé and (2) Yamachiche and Rivière-aux-Glaises, and on the south shore by fish from (3) Anse-du-Fort, and (4) Longue-Pointe and Nicolet. The consistency of the parasitological results suggested some degree of temporal stability in the spatial structure of the perch population of Lake St. Pierre. 2+-3+ perch from Longue-Pointe and Nicolet were repeatedly associated with *Diplostomum* spp., those from Yamachiche with *C. cornutum*, and those from Maskinongé with *E. lateralis*. In addition, 2+-3+ from Maskinongé were always dissociated from *C. cornutum*. The differentiation between Maskinongé and Yamachiche was also observed in young-of-the-year but based on a different series of parasites than adults, which is not unexpected as parasite fauna in perch changes with habitat and ontogenetic diet shift (Johnson et al. 2004). In addition, Anse-du-Fort was differentiated from other sites by its dissociation from *Diplostomum* spp, and association with *R. acus* (L2-L3). Based on five week-old fish, this overall heterogeneous distribution of the parasite fauna of yellow perch in Lake St. Pierre suggests the existence of distinct spawning subpopulations. Furthermore, these subpopulations appear to remain differentiated up to at least the third year.

Depending on the time spent in their host, parasites will provide information at different temporal scales. Because *Diplostomum* spp. can accumulate in a fish's eyes over several years (Chappell 1995), discrimination based on this trematode suggests a long term site fidelity. Indeed, an undifferentiated use of all areas by fish would result in an homogenisation of infection. Presence of *R. acus* at the L2-L3 developmental stages also may indicate a steady association with a site as it can live as long as two years in its intermediate host (Smith 1986). *T. scheuringi*, *B. sacculata*, *C. cornutum* and *E. lateralis* could have a more limited potential to indicate long term site fidelity because their life spans in fish probably do not exceed a year (Thomas 1958; Sandeman and Pippy 1967; Kennedy and Burrough 1977; Marcogliese et al. 2001a; Kennedy 2006). However, the fact that they were discriminating the same sites both in 2004 and 2005 strongly suggests that the subpopulations remained differentiated for at least two years.

Results obtained with parasites and $\delta^{13}C$ in 0+ perch converged as the two techniques discriminated perch from Maskinongé and from Yamachiche. However, while no difference in parasites was observed between 2+-3+ perch from Longue-Pointe and Nicolet, carbon isotope ratios revealed two groups, the former having lower $\delta^{13}C$ values. Parasites and $\delta^{13}C$ in fish are regulated by distinct processes. The distribution and abundance of parasites are related to those of all hosts involved in the parasites' life cycles. Consequently, habitat characteristics that influence the presence of vertebrate and invertebrate potential hosts, such as presence of plant beds or structural complexity (Schneider and Winemiller 2008; Warfe et al. 2008; Shupryt and Stelzer 2009), will play a major role in parasite transmission. For example, based on a survey on eyefluke infection in spottail shiners captured at four localities along the St. Lawrence River, Marcogliese et al. (2001a) related the high abundance of *Diplostomum* spp. observed at one site to the presence of large emergent macrophyte beds, which is suitable habitat for lymnaeiid snails, the first intermediate host. Similarly, the large macrophyte beds occupying extensive areas at the Longue-Pointe and Nicolet sites (Vis et al. 2007) likely support large snail populations, resulting in enhanced *Diplostomum* spp. infections in fish.

$\delta^{13}C$ of dissolved inorganic carbon ($\delta^{13}C_{DIC}$) strongly influences $\delta^{13}C$ of primary producers, whose isotopic signature is transmitted to consumers (Rounick and Winterbourn 1986; Keough et al. 1998). Therefore, the low $\delta^{13}C$ observed in 0+ perch from Yamachiche and 2+-3+ perch from Longue-Pointe in 2005 probably reflects a low $\delta^{13}C_{DIC}$ at the base of their food webs. Differences of $\delta^{13}C_{DIC}$ among sites may result from contrasting biological processes, such as rates of respiration vs. photosynthesis. Indeed, concentrations of dissolved organic carbon and water transit time, two important factors that determine the rates of decomposition and bacterial respiration, and thus $\delta^{13}C_{DIC}$ (Keough et al. 1998; Barth and Veizer 1999), are highly heterogeneous among the different sectors of the lake (Hudon and Carignan 2008).

The more negative $\delta^{13}C$ values in perch could have reflected a zooplankton-oriented diet. In such a case we should have observed a higher abundance of zooplankton-transmitted parasites, such as *Proteocephalus* sp., transmitted by cyclopoid copepods, or *B. sacculata*, transmitted by cladocerans, in perch having lower $\delta^{13}C$. However, not only were these two parasites not a discriminating factor between Longue-Pointe and Nicolet, but the mean abundance of *Proteocephalus* sp. was lower in 0+ perch from Yamachiche than from Maskinongé. This suggests that differences of $\delta^{13}C$ between 0+ perch from Maskinongé and Yamachiche, and between 2+-3+ perch from Longue-Pointe and others in 2005 were not related to the type of prey consumed but rather that 0+ perch from Yamachiche, and 2+-3+ perch from Longue-Pointe relied on a ^{13}C depleted food web compared to other perch of their respective age classes

Comparisons among age classes

Differences within sites of $\delta^{13}C$ between 0+ perch and other age classes were observed. From the time they hatched until the end of May, yellow perch in LSP feeds mainly on zooplankton (Théberge, 2007, see also Chapter III). A diet linked to the zooplanktonic food web can influence $\delta^{13}C$. Indeed, as a result of the effect of the thickness of the boundary layer, which poses resistance to diffusion of dissolved inorganic carbon during uptake by primary consumers (Osmond *et al.* 1981; Rasmussen

& Trudeau 2007) $\delta^{13}C$ of phytoplankton and periphyton can differ locally, the former being generally ^{13}C depleted relative to the latter. Therefore, we have to correct for the zooplanktonic diet of 0+perch to compare their $\delta^{13}C$ with other age classes. In LSP, a relationship between $\delta^{13}C$ zooplanktonic and benthic primary consumers showed that feeding exclusively on zooplankton would shift an individual's $\delta^{13}C$ of -5.40 ‰ compared to a individual having a diet based on benthic invertebrates (Paris et al., in prep) which is consistent with what was observed in other systems (France, 1995). So, correcting for the zooplankton-induced depleted $\delta^{13}C$ in 0+ perch would correspond to a mean $\delta^{13}C$ that would be shift from -30.22 ‰ to -24.82 ‰ at Maskinongé and from -32.40 ‰ to -27.00 ‰ at Yamachiche if those fish were feeding mostly on benthic macroinvertebrates. Thus, even after correction, our $\delta^{13}C$ results suggest that 0+ perch and adults exploited two fundamentally different food web pathways, which is consistent with our knowledge of the biology of yellow perch (Scott and Crossman 1974, Thorpe 1977, Whiteside et al. 1985).

Between years differences

Differences between 2+-3+ perch from Longue-Pointe and Nicolet were observed in 2005 but not in 2004. Because our results are based only on two sampling years, we cannot determine which one of the two situations was unusual. However, the fact that differences in $\delta^{13}C$ between years were observed only at one of the four sampling sites suggest that very localized and temporally variable processes occurred.

Conclusion

Definition of fish stock units is a fundamental requirement for effective resource management as it is the initial step in estimating key population parameters such as growth, mortality, and recruitment. It is therefore suggested that as long as the existence of subpopulations is suspected, it is essential to continue to attempt to define them (Kutkuhn 1981; Begg et al. 1999; Clapp and Dettmers 2004; Deroba and Bence 2008). To date, direct measurements of population characteristics, such as fish length and weight, and RNA/DNA ratio used as index of short-term growth, suggest that the perch

population of Lake St. Pierre is partitioned into at least two subpopulations (Guénette et al. 1994; Tardif et al. 2005; Glemet and Rodriguez 2007). Our results suggest that spawning stocks form at least five distinct units that remain stable at least until fish reach their third year. Consequently, current fishing restrictions should be maintained in every sector of the lake until complete population recovery.

Both parasites and carbon isotope ratios have been successfully used for stock discrimination in large marine ecosystems. However, few studies attempted to identify subpopulations at the scale of a single lake with these indicators (Bowen and Stedman 1990; Balling and Pfeiffer 1997; Hoff et al. 1997; Takai and Sakamoto 1999). Here, we identified within Lake St. Pierre four groups using parasites, and two others using carbon isotopic ratios. By combining the two indicators, we were thus able to identify five distinct units in a perch population that do not differ genetically (Leclerc et al. 2008). Genetic markers may underestimate the degree of population structure because only little movement among units is required to maintain genetic homogeneity (Schrey et al. 2009, Ungfors et al. 2009). Our study showed that contrasting and incomplete results may arise depending on the technique used and emphasize the importance of employing more than a single approach for fish stock units identification when developing conservation and management strategies.

Acknowledgements

We thank A. Gendron for her help in parasitological procedures, A. Bertolo for his help with statistical analyses, R. Bacon, M-E. Deshaies, F. Darchambeau and M. Théberge for their logistic support and assistance in the field, and A-A. Beaudoin, D. Gadbois-Côté, G. Pepin, and J. Trépanier for their technical assistance. This study was supported by grants from the Natural Sciences and Engineering Research Council of Canada and the Canada Research Chairs program to PM. and research funds from the St. Lawrence Action Plan (Environment Canada) to DM.

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Table 1. Results of Canonical Variate Analyses performed to discriminate 2+-3+ perch (2004) and 0+, 1+, 2+-3+ perch (2005) among sites, based on their parasite abundance.

Year	Perch age	Axis	Eigenvalue	Proportion of variance explained	Significance tests P-values for all axis
2004	2+-3+	1	0.397	13.2	0.0001
		2	0.124	17.4	
2005	0+	1	0.275	27.5	0.0001
2005	1+	1	0.294	14.7	0.0003
		2	0.075	18.5	
2005	2+-3+	1	0.287	07.8	0.0001
		2	0.184	11.6	

APPENDIX

Mean abundance, S.D. (in parentheses), and prevalence (%) of parasites found in 2004 and 2005 in yellow perch from Lake St. Pierre at Maskinongé, Yamachiche, Rivière-aux-Glaises, Anse-du-Fort, Longe-Pointe and Nicolet sampling sites.

	Maskinongé				Yamachiche			Rivière-aux-Glaises	Anse-du-Fort		Longue-Pointe		Nicolet	
	2004	2005	2005	2005	2005	2005	2005	2005	2004	2005	2004	2005	2004	2005
	2+-3+	0+	1+	2+-3+	0+	1+	2+-3+	2+-3+	2+-3+	1+	2+-3+	2+-3+	2+-3+	2+-3+
	n = 23	n = 171	n = 21	n = 62	n = 169	n = 16	n = 49	n = 41	n = 20	n = 21	n = 19	n = 56	n = 20	n = 50
Trematoda metacercariae														
Diplostomum spp.	26.35 (28.72) 91	0	1.43 (4.12) 40	31.11 (46.27) 94	0	4.81 (11.50) 60	23.12 (42.43) 90	19.98 (26.51) 90	16.24 (15.4) 90	1.95 (2.71) 52	26.63 (38.47) 100	55.29 (77.21) 100	49.81 (33.12) 100	57.31 (62.74) 98
Tylodelphys scheuringi	3.48 (5.92) 65	0.57 (0.99) 34	3.76 (5.53) 60	2.88 (4.88) 61	0.03 (0.20) 2	1.75 (3.21) 47	0.41 (1.41) 12	0.71 (0.96) 46	2.62 (5.38) 43	0.76 (1.45) 38	5.16 (10.70) 53	5.82 (9.83) 80	4.24 (5.38) 80	2.04 (2.60) 69
Posthodiplostomum spp.	8.57 (34.49 39	<0.01 < 1	0	3.34 (12.03) 25	<0.01 < 1	0.06 (0.25) 7	1.80 (5.17) 22	1.15 (3.28) 20	6.62 (19.03) 24	0	0.32 (0.82) 16	8.54 (38.01) 30	8.43 (20.95) 35	23.37 (72.85) 39
Ornithodiplostomum spp.	0.17 (0.65) 9	0	0.10 (0.30) 10	0.25 (0.72) 15	0	0.06 (0.25) 7	0.27 (0.57) 20	0.63 (1.20) 29	0.05 0.22 5	0.05 0.22 5	0.16 (0.50) 11	0.20 (0.55) 14	0	0.08 (0.39) 0
Apophallus brevis	73.83 (98.47) 100	0.03 (0.17) 3	23.67 (12.89) 100	100.87 (116.88) 99	0.01 (0.11) 1	38.56 (35.9) 100	73.18 (57.43) 100	62.07 (63.32) 100	67.00 (63.28) 95	15.90 (15.46) 100	93.37 (110.05) 95	120.96 (113.89) 100	125.95 (96.56) 95	86.25 (88.30) 98
Tetracotyle spp.	0.57 (1.56) 22	0.01 (0.11) 1	0	0.47 (1.99) 6	0	0	0.39 (1.06) 14	0.49 (2.51) 10	0.24 (0.70) 14	0	0.32 (0.67) 21	0.41 (1.07) 16	0.29 (1.10) 10	1.16 (2.94) 4
Ichthyocotylurus spp.	9.39 (13.02) 83	0.07 (0.36) 5	2.38 (2.64) 80	7.20 (10.74) 71	<0.01 < 1	8.81 (14.96) 73	9.40 (19.95) 82	6.41 (9.57) 71	6.33 (6.32) 67	3.19 (3.43) 76	4.84 (4.14) 84	8.75 (11.09) 82	11.48 (15.27) 80	6.80 (8.66) 71

Trematoda														
Bunodera sacculata	0.13 (0.34) 13	0.07 (0.32) 5	0.57 (2.18) 15	1.56 (4.25) 26	0.10 (0.39) 7	1.00 (1.55) 40	0.61 (1.93) 24	0.32 (0.79) 20	0	0	0.05 (0.23) 5	0.18 (0.77) 7	0	0.02 0.14 2
Crepidostomum cornutum	2.96 (8.83) 35	0.06 (0.28) 5	0	11.56 (31.74) 47	0.03 (0.17) 3	6.44 (8.94) 67	27.86 (35.40) 82	66.22 (145.55) 78	16.67 (39.25) 81	0.81 (2.87) 14	13.79 (16.32) 79	19.09 (26.79) 75	5.00 (5.99) 75	24.06 (29.06) 82
Phyllodistomum superbum	0.70 (2.14) 22	0	1.57 (2.73) 45	1.21 (2.14) 37	0	0.88 (1.31) 47	1.00 (2.01) 37	2.00 (3.07) 56	0.81 (2.42) 24	0.43 (1.03) 19	0.26 (0.56) 21	0.80 (1.68) 36	0.86 (2.31) 25	1.14 (1.99) 41
Azygia angusticauda	0.39 (1.03) 17	0.09 (0.28) 9	0	0.66 (1.73) 21	0.04 (0.22) 3	0.06 (0.25) 7	0.45 (1.02) 22	0.12 (0.40) 10	0.48 (0.60) 43	0.10 (0.30) 10	0.79 (1.51) 32	0.29 (0.76) 16	0.10 (0.30) 10	0.12 (0.48) 8
Nematoda														
Raphidascaris acus (L2-L3)	15.55 (13.91) 91	0	0.29 (0.56) 24	10.92 (12.49) 95	0	1.69 (2.36) 50	11.35 (13.02) 90	12.50 (16.89) 95	15.57 (19.49) 95	1.43 (2.01) 53	14.71 (19.49) 95	17.95 (20.57) 79	13.27 (9.49) 91	27.36 (29.55) 90
Raphidascaris acus (L4) and adults	1.40 (2.60) 27	0	1.43 (0.36) 14	1.31 (3.15) 38	0	0.44 (0.51) 44	0.80 (1.61) 38	1.89 (4.09) 58	1.29 (2.49) 44	0	1.50 (2.49) 53	4.66 (8.13) 73	2.44 (4.99) 43	3.52 (7.62) 64
Cestoda														
Bothriocephalus sp.	0.13 (0.34) 13	0	0	0.13 (0.38) 10	0	0.06 (0.25) 7	0.08 (0.57) 2	0.10 (0.30) 10	0.10 (0.30) 10	0	0.05 (0.23) 5	0.34 (0.92) 16	0.05 0.22 5	0.12 (0.43) 8
Proteocephalus sp.	3.35 (5.17) 57	0.81 (1.43) 36	0.33 (0.80) 20	2.92 (8.29) 28	0.42 (1.31) 17	1.06 (1.65) 47	2.49 (5.87) 47	2.80 (5.02) 61	7.52 (14.94) 57	0.24 (0.89) 10	5.53 (10.77) 47	3.0 (7.16) 45	4.43 (12.20) 50	3.47 (6.46) 61
Acanthocephala														
Echinorhynchus lateralis	0.83 (1.03) 43	0	0.10 (0.44) 5	0.60 (1.18) 26	0	0.06 (0.25) 7	0.20 (0.50) 18	0.10 (0.30) 10	0	0	0	0.07 (0.32) 5	0	0.02 (0.14) 2
Neoechinorhynchus rutili	0.87 (1.63) 39	0	0.24 (1.09) 5	1.48 (3.53) 38	0	0.19 (0.54) 13	0.98 (2.28) 33	0.71 (1.12) 34	0.71 (0.96) 43	0	0.95 (1.31) 47	0.64 (2.74) 21	0.48 (0.93) 35	0.49 (1.05) 27

Annelida														
Hirudinea	1.91 (5.41) 48	<0.01 < 1	0.19 (0.51) 10	0.73 (2.72) 18	<0.01 < 1	0.50 (1.10) 27	0.96 (1.87) 33	0.61 (0.95) 42	0.95 (1.47) 38	0.19 (0.51) 14	0.05 (0.23) 5	0.46 (1.25) 21	0	1.45 (3.12) 31
Mollusca														
Glochidia	14.61 (49.05) 13	1.14 (2.77) 32	13.14 (17.88) 65	13.08 (46.88) 34	0.18 (1.13) 4	15.44 (27.99) 60	18.41 (47.14) 55	23.00 (66.08) 54	64.71 (122.76) 52	8.14 (12.86) 81	25.47 (52.54) 42	4.48 (13.25) 29	12.76 (43.05) 20	14.06 (46.01) 18

Figure legends

Figure 1: Location of yellow perch (*Perca flavescens*) sampling sites in Lake St. Pierre, Québec, Canada

Figure 2: Parasite taxa discriminating perch among sectors. Maskinongé (Maski), Yamachiche (Yam), Rivière-aux-Glaises (RAG) sampling sites are located on the north shore while Anse-du-Fort (ADF), Longue-Pointe (LP), and Nicolet sampling sites are located on the south shore of Lake Saint-Pierre. a) 2+-3+ yellow perch (*Perca flavescens*) captured in 2004, b) 1+ yellow perch captured in 2005, and c) 2+-3+ yellow perch captured in 2005

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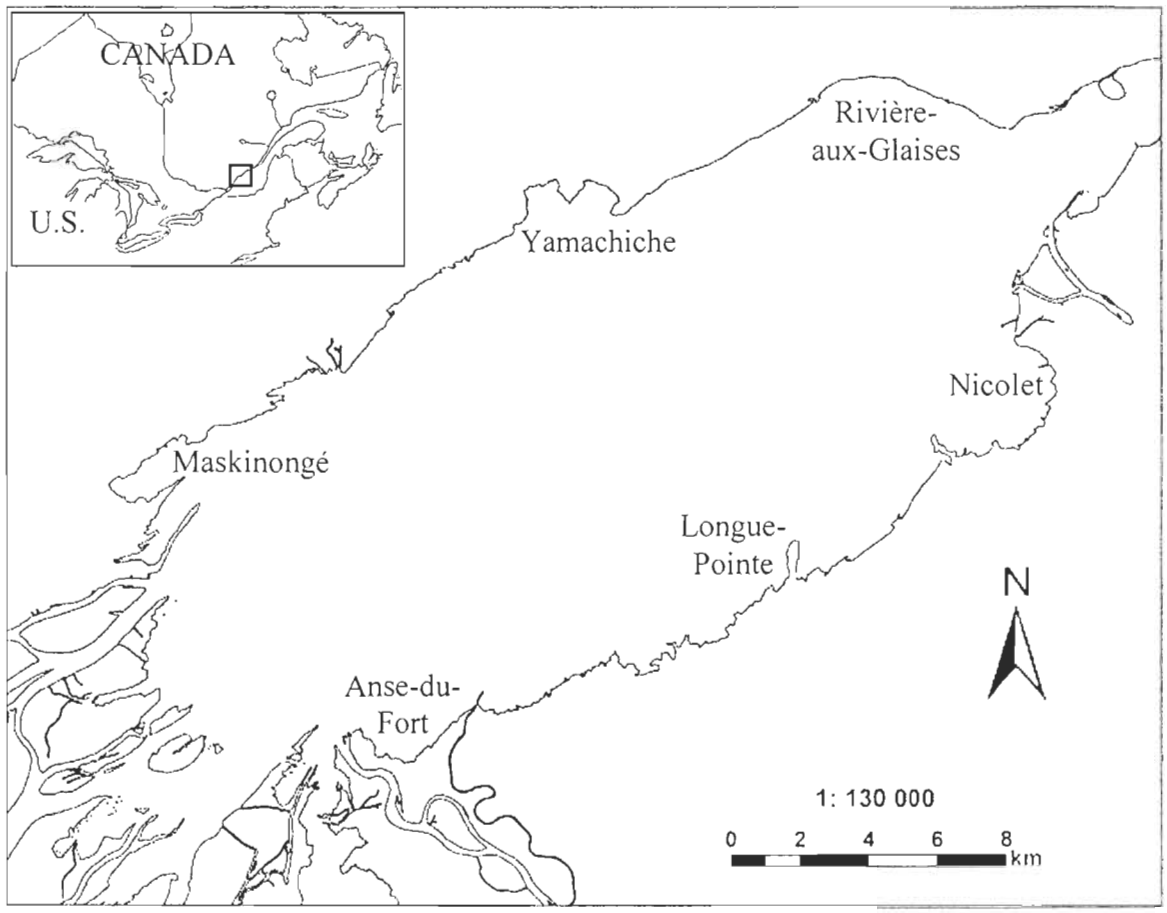
Figure 3: $\delta^{13}C$ values of 2+-3+ yellow perch (*Perca flavescens*) captured in 2004 (dotted boxes), and of 0+ (grey boxes), 1+ (black boxes), 2+-3+ (white boxes) yellow perch captured in 2005 at Maskinongé (Maski), Yamachiche (Yam), Rivière-aux-Glaises (RAG), Anse-du-Fort (ADF), Longue-Pointe (LP), and Nicolet sampling sites in Lake St. Pierre. Each box enclosed 50% of the data, the lower and upper part of the boxes give the estimated 25^{th} and 75^{th} percentiles, and the line in the middle indicates the median value. The upper and lower whiskers are drawn from the box to the most extreme point within 1.5 interquartile range. Values between the 1.5 and 3 interquartile ranges are represented by an asterix. Within each age class, boxes with different letters are significantly different (ANOVA, $p < 0.05$).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km

Figure 1

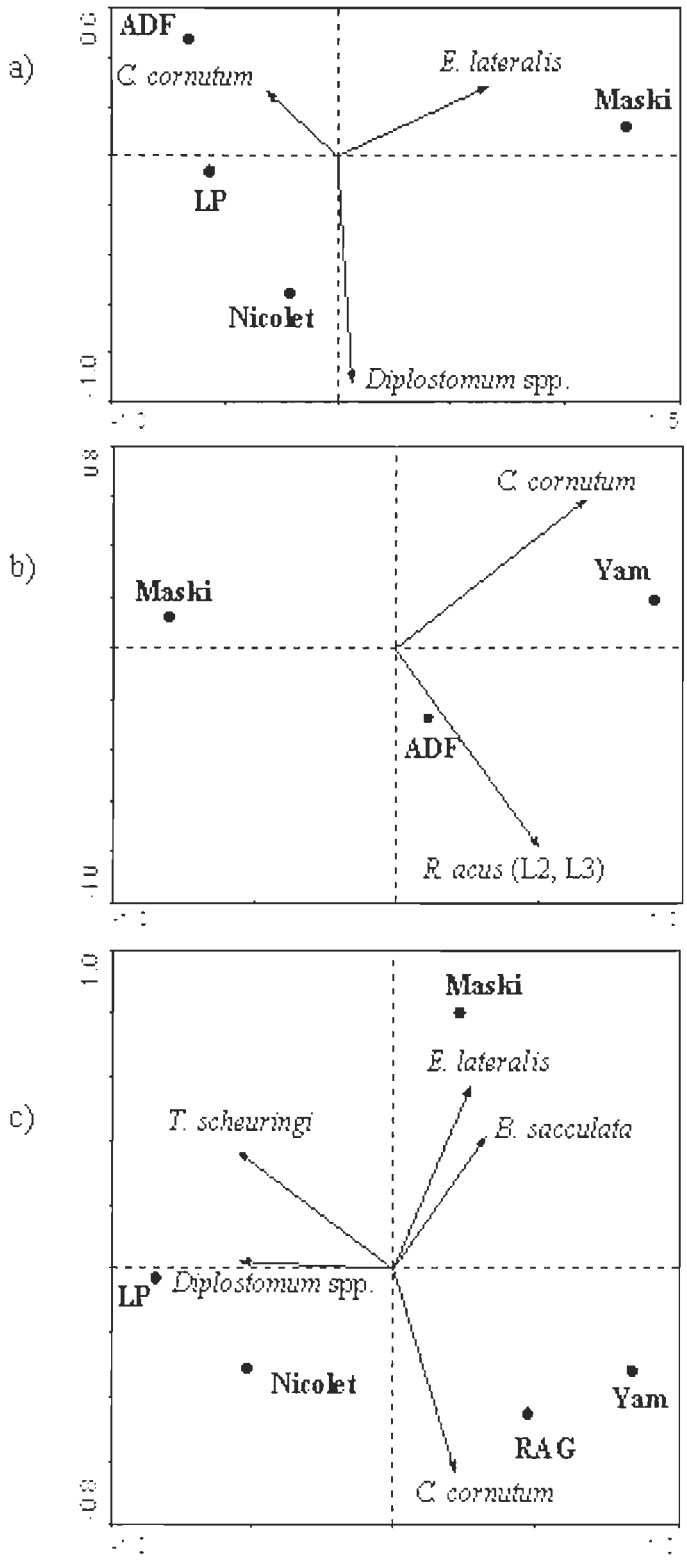
a)
ADF
C. cornutum
E. lateralis
Maski
LP
Nicolet
Diplostomum spp.
b)
C. cornutum
Maski
Yam
ADF
R. acus (L2, L3)
c)
Maski
E. lateralis
T. scheuringi
B. sacculata
LP
Diplostomum spp.
Nicolet
Yam
RAG
C. cornutum

Figure 2

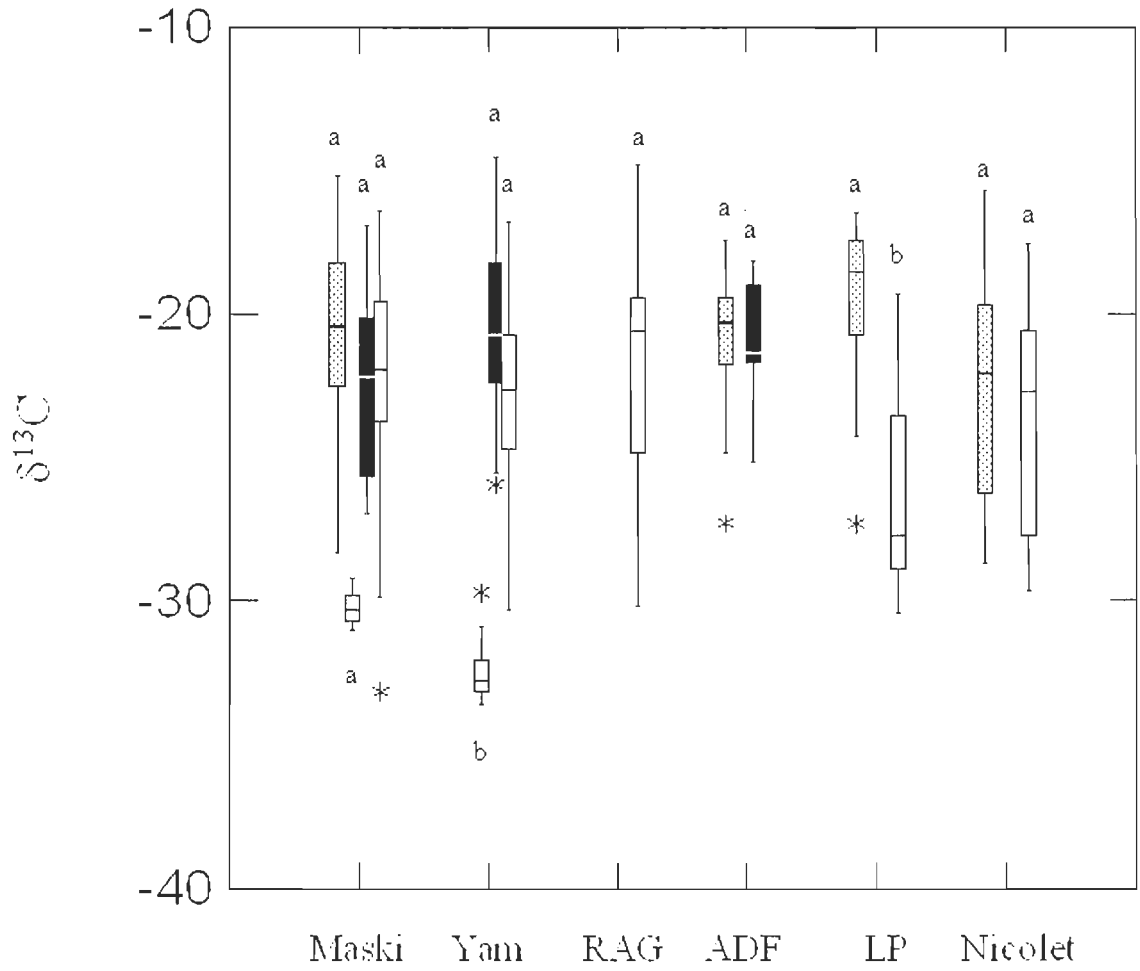

Figure 3

CHAPITRE III

ESTIMATION DE L'ÉTENDUE DE L'HABITAT D'ALIMENTATION DE LA PERCHAUDE DANS UN LAC FLUVIAL À L'AIDE D'UN GRADIENT DU $\delta^{13}C$ ET DES PARASITES

ESTIMATING THE FEEDING RANGE OF YELLOW PERCH IN A FLUVIAL LAKE USING $\delta^{13}C$ GRADIENTS AND PARASITES

Résumé

1. Parce qu'elle détermine l'échelle spatiale des interactions prédateurs-proies, l'étendue de l'habitat d'alimentation d'un individu est au centre de la dynamique des réseaux trophiques. Cependant, bien que son importance soit reconnue, l'étendue de l'habitat d'alimentation est rarement établie parce qu'il est difficile d'obtenir des informations détaillées sur les interactions trophiques.

2. Les marqueurs biologiques sont utiles dans les études spatiales pourvu qu'il y ait une hétérogénéité spatiale à l'intérieur du secteur étudié. Étant formé de trois masses d'eau ayant des caractéristiques physiques et chimiques contrastantes, le lac Saint-Pierre, un lac fluvial du Saint-Laurent, offre une opportunité unique de déterminer l'étendue de l'habitat d'alimentation des perchaudes (*Perca flavescens*) à l'aide du $\delta^{13}C$. Toutefois, puisque les réseaux trophiques qui dépendent du phytoplancton ont généralement un $\delta^{13}C$ plus négatif que ceux qui dépendent du périphyton, il est essentiel pour interpréter correctement des patrons spatiaux de déterminer la contribution du zooplancton dans le régime alimentaire d'un poisson,. Nous avons utilisé les parasites des perchaudes pour examiner si leur $\delta^{13}C$ reflète le $\delta^{13}C$ à la base du réseau trophique plutôt qu'une spécialisation alimentaire axée sur le zooplancton. Les parasites ont également été utilisés pour examiner les changement ontogéniques du régime alimentaire, alors que le $\delta^{15}N$ a été utilisé pour examiner les changements de position trophique.

3. Le $\delta^{13}C$ des consommateurs primaires était très variable et affichait un fort gradient le long de l'axe rive-chenal, ce qui suggère qu'au lac Saint-Pierre, le $\delta^{13}C$ peut refléter la position spatiale d'un individu.

4. Ce fort gradient isotopique nous a permis d'inférer les mouvements de la perchaude. En comparant la variabilité du $\delta^{13}C$ des perchaudes à celle des

consommateurs primaires, nous avons estimé que l'étendue de l'habitat d'alimentation des perchaudes adultes était de 3 km sur l'axe rive-chenal.

5. Cette étendue linéaire n'a pas augmenté entre les classes d'âge 1+-3+. Par ailleurs, le $\delta^{15}N$ des perchaudes et les parasites indiquaient qu'il n'y avait pas d'augmentation de position trophique et qu'il n'y avait pas de changements de régime alimentaire entre ces mêmes classes d'âge, ce qui suggère que les augmentations généralement observées dans les relations allométriques interspécifiques entre le domaine vital d'un poisson et sa taille pourraient être reliées à la position trophique.

6. L'utilisation combinée des rapports isotopiques et des parasites nous a permis de déterminer qu'au lac Saint-Pierre, la population de perchaudes adultes utilise un grande partie des habitats localisés entre la plaine inondable et la rivière principale mais que chaque individu exploite un secteur restreint.

Abstract

1. The feeding range of an individual is central to food web dynamics as it determines the spatial scale of predator-prey interactions. However, despite recognition of its importance as a driving force in fish population dynamics, establishing feeding range is seldom done as detailed information on trophic interactions are difficult to obtain.

2. Biological markers are useful in spatial studies as long as a spatial heterogeneity is present within the area investigated. Being composed of three main water masses with contrasting physical and chemical characteristics, Lake St. Pierre (LSP), a fluvial lake of the St. Lawrence River, offered a unique opportunity to determine the feeding range of individual yellow perch (*Perca flavescens*) using $\delta^{13}C$. However, because food chains based on phytoplankton have generally more negative $\delta^{13}C$ then those depending on periphyton, it was essential to determine the contribution of zooplankton in fish diet in order to correctly interpret spatial patterns of $\delta^{13}C$. We used parasites in perch to examine if their $\delta^{13}C$ was reflecting local $\delta^{13}C$ baseline conditions rather than a feeding specialization on zooplankton. Parasites were also used to examine diet ontogenetic shift, while $\delta^{15}N$ was used to examine shift in trophic position.

3. $\delta^{13}C$ of primary consumers was highly variable and exhibited a striking gradient along the shore-channel axis, suggesting that in LSP, $\delta^{13}C$ may reflect an individual's spatial position.

4. This strong isotopic gradient allowed us to make inferences about movements of yellow perch. By comparing yellow perch variability in $\delta^{13}C$ to that of primary consumers, we estimated that the adults feeding range was around 3 km on the shore-channel axis.

5. Linear ranges did non increase between 1+-3+ age classes. However, perch $\delta^{15}N$ and parasites indicated that no increase of trophic position and no diet shift

occurred among these same age classes, suggesting that the usual increases observed in interspecific allometric relationships between fish home range to body size could be related to trophic position.

6. The combined use of isotopic ratios and parasites allowed us to determine that in LSP, the adult population uses a wide range of habitats between the floodplain and the main channel. However, individually, each perch exploit a restricted area.

Keywords :

biological tag, feeding habitat, food web dynamic, parasite, river-floodplain systems, spatial gradient, stable isotopes

Introduction

The spatial scale of interactions among organisms is generally recognized as being of fundamental importance to ecology (Addicott *et al.* 1987). The feeding range of an individual can be defined as "the region within which an organism is active or has some influence during the appropriate period of time" (Addicott *et al.* 1987). This ecological attribute is central to food web dynamics as it not only determines the spatial scale of predator-prey interactions (DeAngelis & Petersen 2001) but also by coupling food webs in space it may have strong impacts on their stability (de Roos *et al.* 1998; McCann *et al.* 1998). For example, it has been hypothesized that the wide-ranging feeding of avian predators plays a key role in synchronizing populations of microtine rodents in northern latitudes (Ims & Steen 1990). In aquatic systems, feeding range typically increases with body size (e.g. Minns 1995; McCann *et al.* 1998). However, substantial unexplained variance, spanning close to one order of magnitude, is observed around these allometric relationships. Feeding range of individuals occupying lower quality feeding habitats are likely to range more widely than those feeding in areas where the density and quality of prey are high (Kramer & Chapman 1999; Laurel *et al.* 2004). Therefore, feeding range may differ among populations as it may depend on ecosystem productivity or some other ecological characteristics (Minns 1995, Woolnough *et al.* 2009).

Despite recognition of its importance as a driving force in fish population dynamics, establishing feeding range in real ecosystems is seldom done as detailed information on trophic interactions and fish movement are difficult to obtain for individuals. This problem is compounded in highly dynamic ecosystems such as large river-floodplain systems as they are spatially and temporally dynamic, both longitudinally and laterally. Integrated theories have been proposed to identify energy flow patterns in these complex systems (Vannote *et al.* 1980; Junk *et al.* 1989; Thorp & Delong 1994). However, none of them explicitly addressed the spatial scale of trophic interactions.

Because it is a conservative tracer along the food chain, with little fractionation associated with trophic transfer (DeNiro & Epstein 1978), carbon stable isotope ratios

($\delta^{13}C$) can be a powerful tool to identify spatial patterns in resource use by fish. For example, $\delta^{13}C$ was used to assess site fidelity and residency (Takai & Sakamoto 1999; Gray *et al.* 2004; Cunjak *et al.* 2005), and trace movements and migration in fish (Guelinckx *et al.* 2006; Rasmussen *et al.* 2009). However, one constraint arises from using $\delta^{13}C$ to study feeding ranges when food webs are potentially supported by both phytoplankton and periphyton. $\delta^{13}C$ of these food sources can differ locally as a result of the effect of the thickness of the boundary layer, which poses resistance to diffusion of dissolved inorganic carbon during uptake by primary consumers (Osmond *et al.* 1981; Rasmussen & Trudeau 2007). Consequently, phytoplankton is generally ^{13}C depleted relative to benthic primary producers, and food chains based on phytoplankton have more negative $\delta^{13}C$ then those ultimately depending on periphyton (Hecky & Hesslein 1995). It is, therefore, essential to independently determine the contribution of zooplankton to fish diet in order to correctly interpret spatial patterns in fish $\delta^{13}C$. Being linked to the local occurrence of their hosts, trophically-transmitted parasites are good indicators of individuals' diet (Knudsen *et al.* 1996; Bertrand *et al.* 2008; Valtonen *et al.* 2010). Not only parasites have the advantage to provide information even when stomach are empty (Baldwin *et al.* 2008), but they also indicate long-term feeding as they can accumulate in their hosts for months or longer (Marcogliese and Cone, 1997).

Another limitation when using $\delta^{13}C$ as markers in spatial studies is that a clear biogeochemical spatial heterogeneity has to be present within the feeding area of the target population (Guelinckx *et al.* 2006; Rasmussen *et al.* 2009). Strong spatial gradients in $\delta^{13}C$ will increase the power of delineating feeding range of individuals. Studies on the St. Lawrence River (Québec, Canada) showed that owing to their equilibration with the atmosphere and contact with carbonate-rich sediments, waters from the main channel coming from the Great Lakes have higher dissolved inorganic carbon $\delta^{13}C$ ($\delta^{13}C_{DIC}$) values than those of the north and south tributaries which are highly influenced by bacterial respiration (Yang *et al.* 1996; Barth & Veizer 1999). Lake St. Pierre (LSP), a 350 km^2 fluvial lake of the St. Lawrence River is bordered by an

extensive floodplain and displays large environmental spatial variations typical of such river-floodplain systems (Sparks 1995; Amoros & Bornette 2002). Therefore, LSP, by its unique geographical location, may provide us with a powerful opportunity as three main water masses flow side by side with little lateral mixing (Frenette *et al.* 2006; Vis *et al.* 2007; Hudon & Carignan 2008). The central water mass is formed by waters from the Great Lakes, while those flowing along the north and south shores are formed by tributaries of low $\delta^{13}C_{DIC}$ (Yang *et al.*, 1996).

This study aimed to establish the feeding range of yellow perch (*Perca flavescens*) of LSP using $\delta^{13}C$. Until recently, this population was the target of extensive commercial and recreational fisheries in LSP, but its collapse led to strict harvest regulations since 1997 (Magnan, 2002). We hypothesized that the contrasting environmental conditions of LSP may produce a biogeochemical gradient on the shore-channel axis that could be used to develop a simple spatial model evaluating the feeding range of yellow perch. To address our objectives, we first examined if $\delta^{13}C$ of benthic primary consumers with low mobility followed a spatial gradient on the shore-central area axis of the lake. Then, we examined the relationship between the $\delta^{13}C$ of low mobility invertebrate predators (odonates) and that of the primary consumers to establish how food chains with predators having little mobility tracked the local baseline isotopic signal. Next, in order to establish yellow perch feeding range within LSP, we compared their variability in $\delta^{13}C$ to that of primary consumers following an approach recently suggested by Rasmussen *et al.* (2009). Moreover, because habitat range is related to size and trophic position (Harestad & Bunnell 1979; Linfield 1985; Minns 1995), we used primary consumers and perch $\delta^{15}N$, typically higher of 3-4 ‰ in a consumer than in its prey (Minagawa & Wada 1984; Peterson & Fry 1987), to determine if the feeding range of perch were related to age or trophic position. Finally, we examined parasites in yellow perch to examine if their $\delta^{13}C$ was reflecting local $\delta^{13}C$ baseline conditions rather than a feeding specialization on zooplankton.

Material and methods

Study Site

LSP (Québec, Canada) is shallow (average depth at mean discharge approx. 3 m) except in the dredged central navigation channel (depth approx. 11 m). Waters flowing along the north shore mainly originates from the Ottawa River and are rich in nutrients, suspended particulate organic matter (SPOM), and dissolved organic carbon (DOC). The central part, occupied by relatively clear hard waters coming from the Lake Ontario, are characterized by low DOC and SPOM. The water mass flowing along the south shore, formed by inflows from tributaries draining agricultural watersheds (Richelieu, Yamaska, and St. François rivers) have low SPOM concentrations, but are rich in nutrients, chl *a*, and DOC (Frenette *et al.* 2006; Vis *et al.* 2007; Hudon & Carignan 2008). Six sites along the north (Maskinongé, Yamachiche and Rivière-aux-Glaises) and south (Anse-du-Fort, Longue-Pointe and Nicolet) shores were selected for perch sampling (Fig 1).

Yellow perch and invertebrate sampling

Adult yellow perch were obtained on their spawning grounds, from 23 to 30-04-04 and 18 to 08-05-05, from commercial fishers except at Rivière-aux-Glaises where no commercial fishing occurs. At this location, we captured perch with gear (fyke nets) and techniques similar to those used by commercial fishers. We also captured 0+ perch at Maskinongé and Yamachiche sites with a seine on 30-06-05. Because only few centimetres of water remain in the floodplain areas after spring flood, our sampling locations for 0+ perch were shifted relatively to spring sampling of approximately one km toward the centre of the lake.

Benthic macroinvertebrates were sampled from 20 May to 18 June 2004 and from 15 to 24 August 2004 with a dredge pulled with a boat over 100 m parallel to the shore, near the perch sampling sites, and at approximately 1 km and 2-2.5 km offshore, which resulted in 36 sampling locations. After collection, fish and invertebrates were kept on ice until frozen at -4° C within 8 h of collection.

Parasitological and isotopic analysis

Fish weight (± 0,01 g) and length (± 1 mm) were measured after thawing. We determined yellow perch age from annuli on operculum (Baker & McComish 1998). We examined parasites on 340, 58, 280, and 44 of 0+, 1+, 2+, and 3+ individuals respectively. With the exception of blood and nervous system, all organs and tissues were examined for parasites with a dissecting microscope. All parasites encountered were removed, fixed in ethanol 75% and were identified to species or genus (Schmidt 1970; Arai 1989; Gibson 1996; Hoffman 1999) following standard procedures, including staining and mounting. Parasites taxa transmitted by diet were grouped according to the type of intermediate hosts involved in their life cycle. The number of parasites belonging to these groups was calculated for each fish and the percent of each group was calculated for each age class.

After thawing, invertebrates were sorted and identified to genus according to Merritt and Cummins (1996), except for chironomids which were identified to the family level. To determine the $\delta^{13}C$ and $\delta^{15}N$ values of primary consumers at each sampling location, we subsampled chironomids (Diptera), *Gammarus* sp. (Amphipoda) and *Amnicola* sp. (Gastropoda) because those three taxa were simultaneously present at 28 of our sampling sites, while either *Gammarus* sp. or *Amnicola* sp. were absent at the remaining 8 sites. *Amphiagrion* sp. (Odonata), found in 23 of the 36 sampling sites, was also subsampled as representative of low mobility predators. Shells of gastropods were removed. At each sampling site, 10 to 20 individual primary consumers of the same taxon were pooled, and this was done with two or three of the selected taxa (chironomids, *Gammarus* sp., *Amnicola* sp.) while for odonates only three to five individuals were pooled. The $\delta^{13}C$ and $\delta^{15}N$ values representing primary consumers of a sampling site was the mean $\delta^{13}C$, or $\delta^{15}N$, of those two or three taxa.

Additional isotopic data of invertebrates collected from 12 stations in 2006 (Paris *et al.*, unpublished data) completed our characterisation of the isotopic baseline of LSP. Taxonomic groups included in this latter data set were the gastropods *Goniobasis*

livescens and *Planorbella trivolvis,* and *Gammarus fasciatus* (Amphipoda). Sampling and sample preparation followed the 2004 protocols.

For isotopic analyses, a piece of dorsal muscle was taken from adult yellow perch while, because of their very small size, the whole body was used for 0+ perch. For this age group, isotopic analysis were made only on 17 (Maskinongé) and 16 (Yamachiche) individuals randomly selected among those that were parasitized by at least one parasite of any taxon. Fish samples and pooled invertebrates were dried at 60° C for at least 48 hours, ground into a homogeneous powder, and sent for isotopic analysis at the University of New Brunswick where they were analysed with a Finnigan Delta Plus Costech 4010 mass spectrometer. The precision of the mass spectrometer calculated from duplicates of 28 samples was $\leq 0.2‰$.

Statistical analysis

To develop our spatial model of baseline $\delta^{13}C$, we first tested the hypothesis that the $\delta^{13}C$ of benthic primary consumers would be influenced by their distances from the two end-members represented by the high $\delta^{13}C$ main channel and the low $\delta^{13}C$ shore habitat using least-squares regression analysis. Given the spatial configuration of the shore with respect to the main channel in LSP these two distances ("S" and "C") were not strongly collinear (Pearson correlation, $r = -0.37$, $p = 0.01$). For example, some sampling sites could be near shore but at varying distances from the main channel (Fig 1). S and C were established by calculating on a digitalized bathymetric map (chart datum level + 3 m) the linear distance (km) of their sampling locations from the shore and from the navigation channel. Next, we used multiple regression relating benthic invertebrate $\delta^{13}C$ to S and C to ascertain the strength of the spatial gradient in baseline $\delta^{13}C$. Terms of interactions were included to determine if there was an effect of the year or of the sampling month.

Analysis of Variance (ANOVA) followed by *post hoc* Bonferroni test was performed to examine differences of yellow perch $\delta^{13}C$ among sampling sites, and differences of trophic positions among age groups.

A biplot relating $\delta^{13}C$ and $\delta^{15}N$ of primary consumers and of yellow perch suggested a spatial gradient of $\delta^{15}N$ that could be tracked by their $\delta^{13}C$. Therefore, to estimate perch trophic position, we calculated a predicted $\delta^{15}N$ value for each fish from the relationship relating $\delta^{13}C$ and $\delta^{15}N$ of primary consumers. We also examined the relationship between primary consumers' $\delta^{15}N$ and their distance from the shore and from the channel with a multiple regression analysis.

Regression analyses were used to examine relationships between $\delta^{13}C$ and $\delta^{15}N$ of primary consumers, between $\delta^{13}C$ of invertebrate predators (odonates) and primary consumers, and between yellow perch total length, or $\delta^{13}C$, and their trophic position. All analyses were performed using SAS (version 9.1, SAS Institute, Cary, North Carolina)

To estimate the linear feeding range (β, in km) of 1+-3+ yellow perch from $\delta^{13}C$ data we used version 2 of the model presented by Rasmussen *et al.* (2009). Briefly, if a consumer moves very little its isotopic signature should closely track the isotopic spatial gradient, if present, of its resource over the whole distance considered (ΔX, in km). Thus the spatial variance in $\delta^{13}C$ of consumer should be very close to that of its resource. Conversely, large movement patterns by a consumer over the whole gradient in resource isotopic signature would result in all individuals converging toward the mean $\delta^{13}C$ of resources with little inter-individual variance observed. The functional regression (Reduced Major Axis (RMA), Sokal & Rohlf 1995) describes this relationship between consumer and resource $\delta^{13}C$. The RMA slope (q) of this relationship is estimated by the ratio of the standard deviation of the consumer, (SD_c $\delta^{13}C$) over that of the resource (SD_r $\delta^{13}C$) (Sokal & Rohlf 1995). Then, following Rasmussen *et al.* (2009):

$$\beta = (1-q)\,\Delta X \qquad \text{(eq 1)}$$

Here ΔX, the distance over which the gradient in resource (the invertebrate $\delta^{13}C$ signal) is observed was estimated at 5.4 km which is the average distance between the

channel and shore in LSP over the studied area. Feeding ranges were separately estimated for the 1+, 2+ and 3+ age classes.

Results

Invertebrate $\delta^{13}C$

$\delta^{13}C$ of primary consumers was highly variable, ranging from -37.70 to -14.35 ‰, and exhibited a strong gradient along the shore-channel axis increasing from the most negative $\delta^{13}C$ values very close to shore (Fig 2a) to the least negative $\delta^{13}C$ nearer the main channel (Fig. 2b).

Multiple regression analysis showed that both C and S contributed ($p < 0.0001$) to predicting $\delta^{13}C$ of primary consumers ($r^2 = 0.58$; $\delta^{13}C = -16.96 + 2.46$ S (S.E.= 0.76) – 2.35 C (S.E.=0.48); n = 48), with no effect of the year or the sampling month. Thus, primary consumers $\delta^{13}C$ followed spatial gradients from shore to channel averaging 2.4 ‰ km^{-1}(average of the two coefficients in the multiple regression).

$\delta^{13}C$ of predatory invertebrates (odonates) was very strongly related to $\delta^{13}C$ of primary consumers collected at the same site (linear regression, $r^2 = 0.94$, $p < 0.0001$; Fig 3). The range and variance of odonate $\delta^{13}C$ across all our sites (-35.57 to -14.74 ‰, S.D. = 6.04) was very similar to that of primary consumers (-38.42 to -13.22 ‰, S. D. = 7.70).

Yellow perch $\delta^{13}C$ and feeding range

The range of 1+-3+ yellow perch $\delta^{13}C$ (-33.2 to -14.6 ‰) was almost as wide as that of invertebrates with only the very negative values observed in this latter group being missing in fish (Fig 4). $\delta^{13}C$ values of 0+ perch, which were collected only at Maskinongé and Yamachiche, were more negative and had a smaller range than adults (-33.6 to -29.2 ‰). However, this could not be attributed to an effect of the sampling sites because the $\delta^{13}C$ of adult perch captured at Maskinongé and Yamachiche was similar in range and values to those captured at the other sites, with the exception of 2+-3+ perch

from Longue-Pointe (2005) which were more negative than 2+-3+ perch from all other sites (ANOVA, $p < 0.0001$, $r^2 = 0.14$; Fig 5). Estimated linear feeding ranges for the three age classes of adult fish were very close to each other (2.7-3 km) (Table 1).

$\delta^{15}N$ in primary consumers and perch trophic position

$\delta^{15}N$ of primary consumers was related to the distance from the channel (Regression analysis; $r^2 = 0.21$; $\delta^{15}N = 10.18 + -0.55$ C; $n = 48$; Fig 6) but not to the shore. The relationship between $\delta^{15}N$ and $\delta^{13}C$ of primary consumers (pc) was significant (Regression analysis, $r^2 = 0.34$, $p < 0.0001$, $n = 48$), and resulted in the following linear model:

$$\delta^{15}N_{pc} = 11.70 + 0.16\ \delta^{13}C_{pc} \qquad \text{(eq 2)}$$

This model was used as follow to establish a predicted baseline $\delta^{15}N$ value for each fish:

$$\delta^{15}N_{predicted} = (11.70 + 0.16\ \delta^{13}C_{perch}) \qquad \text{(eq 3)}$$

The trophic position of each fish was then calculated using the equation

$$TP_{perch} = ((\delta^{15}N_{perch} - \delta^{15}N_{predicted}) / 3.4) + 2 \qquad \text{(eq 4)}$$

where 3.4 is the expected $\delta^{15}N$ increase between each trophic level (Minagawa and Wada, 1984), and 2 is the trophic position of benthic primary consumers.

The relationships between perch total length, or $\delta^{13}C$, and their trophic position were significant but with low predictive power (Regression analysis, $r^2 = 0.05$ and 0.03 respectively, $p < 0.001$), and this, only when 0+ perch were included in the analysis. Moreover, the only difference in trophic positions among age groups occurred between 0+ and others, where 0+ (TP = 3.21) < 1+ (TP = 3.46) = 2+ (TP = 3.48) = 3+ (3.51) (ANOVA, r^2: 0.07. $p < 0.001$).

Parasitological analysis

Nine trophically-transmitted parasites taxa were identified in yellow perch from LSP. Among them, three were transmitted by ingestion of zooplanktonic cyclopoid

copepods (*Proteocephalus* sp. and *Bothriocephalus* sp.) or cladocerans (*Bunodera sacculata*), one by ingestion of a trematode cercariae (*Azygia angusticauda*), and five by ingestion of various larvae of aquatic insects or crustaceans (*Raphidascaris acus*, *Crepidostomum cornutum*, *Phyllodistomum superbum*, *Neoechinorhynchus rutili*, *Echinorhynchus lateralis*) (Hoffman, 1999).

A clear shift in the pattern of infection occurred between 0+ perch and other age classes, the former being mostly infected by parasites transmitted by zooplankton, and the latter by those using macroinvertebrates (Fig 7). No relationship between $\delta^{13}C$ and the percent of zooplankton-transmitted parasites infecting a fish was observed (Fig 8).

Discussion

Invertebrate $\delta^{13}C$

A strong $\delta^{13}C$ gradient of benthic primary consumers was observed along the shore-channel axis suggesting that in LSP, $\delta^{13}C$ reflects spatial distribution of individuals, with lighter values near-shore and heavier values near the river channel. This gradient may arise from a combination of abiotic and biotic factors. Waters masses flowing along the north and south shores come from tributaries having ^{13}C depleted dissolved inorganic carbon (DIC) compared to the river channel, occupied by waters from the Great Lakes. Indeed, recorded $\delta^{13}C_{DIC}$ values at the outflow of Lake Ontario, the most downstream lake of the Great Lakes system, ranged between -1.6‰ and 2.2‰ (Yang *et al.* 1996; Barth & Veizer 1999) while values of the main LSP tributaries varied between -6‰ and -10.4‰ (Yang *et al.* 1996). Furthermore, the shallow waters along the shores of LSP are characterized by high concentrations of dissolved organic carbon and long transit time (Hudon & Carignan 2008). These conditions promote high rates of decomposition and bacterial respiration (Welcomme 1979) which may result in low $\delta^{13}C_{DIC}$ (Fourqurean *et al.* 1997; Keough *et al.* 1998; Barth & Veizer 1999). Therefore, it is most likely that in near-shore areas, the initial low $\delta^{13}C_{DIC}$ of waters entering the lake combined with local biogeochemical processes resulted in low $\delta^{13}C_{DIC}$ values compared

to that of the low transit time waters of the river main channel. As $\delta^{13}C_{DIC}$ strongly influences $\delta^{13}C$ of primary producers and consumers (Hecky & Hesslein 1995; Keough *et al.* 1998; Finlay *et al.* 1999), the contrasting values between the shores and the channel should be reflected locally by the invertebrate fauna. Similarly, depleted $\delta^{13}C$ values were observed in the entire food web of a wetland relative to adjacent offshore waters of Lake Superior (Keough *et al.* 1996). In both habitats, $\delta^{13}C$ of phytoplankton, invertebrates and vertebrates was related to $\delta^{13}C_{DIC}$.

The strong relationship between $\delta^{13}C$ of odonates and benthic primary consumers $\delta^{13}C$ clearly illustrates how the $\delta^{13}C$ of a predator of low mobility tracks the local baseline isotopic signal. In LSP, the range in both primary consumer and odonates $\delta^{13}C$ observed over a relatively short distance from shore (less then 5 km, Fig.1) spanned more than 21‰ (-38 to -13, and -35 to -14 ‰ for each group, respectively). This range in isotopic signature exceeded that observed in a continent-scale compilation of temperate and Arctic streams and rivers (Finlay 2001). This striking isotopic gradient in LSP is a key feature that allows inferences to be made about movements of consumers in this river-floodplain ecosystem.

Yellow perch $\delta^{13}C$ and feeding range

According to results using parasites, zooplankton occupied a small proportion in the diet of adult yellow perch. This low zooplanktivory therefore was likely not a confounding factor in our interpretation of their $\delta^{13}C$. Indeed, no relationship was observed between adult perch $\delta^{13}C$ and the percent of zooplankton-transmitted parasites. Therefore, $\delta^{13}C$ of adult perch can be compared to that of our baseline estimated from benthic primary consumers.

On the basis that in LSP, $\delta^{13}C$ of an individual is related to its location on the shore-channel axis, our results indicate that the adult population used a wide range of habitats between the floodplain and the main channel, but also that individually, each perch exploits restricted areas. Because $\delta^{13}C$ in fish muscle is time-integrative, (Hesslein

et al. 1993; Harvey *et al.* 2002), the wide range of $\delta^{13}C$ observed suggests that after spawning, adults dispersed all over the lake and no important movements subsequently occurred. Using enclosures along a spatial gradient, Haas et al. (2009) showed that fish had $\delta^{13}C$ and $\delta^{15}N$ values characteristic of each location, and the range along the spatial gradient of the $\delta^{13}C$ and $\delta^{15}N$ of stationary fish was considerably wider than that of wild fish moving along this spatial gradient. Our estimates of linear feeding ranges of adult yellow perch (Table 1) indicate that individuals derived their carbon over a distance of around 3 km between shore and the channel. However, it is difficult to estimate the area used by each individual as the one-dimensional gradient does not allow a tracking of movement parallel to shore. Linear ranges did not increase between 1+, 2+ and 3+ age classes. This result contrast with the usual increases observed in interspecific allometric relationships between fish home range to body size (e.g. Minns 1995). However, trophic position also did not increase with body size in yellow perch among the same age classes. This latter result may suggest that intraspecific variation in home range is not sensitive to size *per se*, but could be related to trophic position.

$\delta^{13}C$ in 0+ yellow perch contrasts with that of adults by its narrow range and by its very negative values. Their strong dependence on a zooplankton diet is likely to influence these values. Indeed, the parasitological results indicated that at least 80% of 0+ perch diet was composed of zooplanktonic organisms. Thus, to relate $\delta^{13}C$ of 0+ perch to our baseline, it is necessary to correct for their feeding specialization on zooplankton. In LSP, a relationship between $\delta^{13}C$ of zooplanctonic and of benthic primary consumers showed that feeding exclusively on zooplankton would shift an individual's $\delta^{13}C$ -5.4 ‰ compared to an individual having a diet based on benthic invertebrates (Paris *et al.*, unpublished data). Correcting for the zooplankton-induced depleted $\delta^{13}C$ in 0+ perch would correspond to a mean $\delta^{13}C$ that would shift from -31.08 (SD: 1.36) (our observed value) to -25.68‰ if those fish were feeding mostly on benthic macroinvertebrates. When related to $\delta^{13}C$ of our baseline, the negative values and the small range of $\delta^{13}C$ could indicate that after hatching, all young perch remained near-

shore and fed only in these areas. However, this would not be in accordance with what is known about the biology of yellow perch. Soon after hatching, larvae are known to move offshore and to come back inshore after about 4 weeks (Whiteside *et al.* 1985). Therefore, $\delta^{13}C$ values in our approximately 5 weeks-old fish could represent the integration of the $\delta^{13}C$ of the prey ingested during such migrations.

Primary consumers $\delta^{15}N$

A relationship was observed between $\delta^{15}N$ of grazers and their distance from the channel. However, the spatial pattern was not as clear as with $\delta^{13}C$. The relationship with the channel had a lower predictive power than with $\delta^{13}C$ and no relationship with the distance from the shore was observed. A few nonexclusive hypotheses may explain this result. It is possible that in LSP, factors influencing $\delta^{15}N$ of primary producers, such as the load of N inputs (Anderson & Cabana 2006), were too variable for a strong spatial pattern to emerge, especially in floodplain areas. Indeed, within a single year, Hudon and Carignan (2008) observed, high lateral as well longitudinal temporal variations of NO_3-N concentrations in the water masses flowing on either side of the channel. By contrast, these variations were low in the channel itself. As NO_3-N concentrations are related to $\delta^{15}N$ of the biota (Diebel & Vander Zanden 2009), this may explain why there may be a relationship between $\delta^{15}N$ of primary consumers and the distance from the channel, but not from the shore. Besides, the composition of benthic algal assemblages was reported to be highly variable in the floodplain among wetland areas, including the presence of cyanobacteria in some sectors (Huggins *et al.* 2004; Vis *et al.* 2008). The possibility of differential fractionation during N assimilation among plant species (Needoba *et al.* 2003, Troxler & Richards 2009), combined with the presence of potentially light $\delta^{15}N$ cyanobacteria in some sectors (Minagawa & Wada 1986; Lehmann *et al.* 2004; Bauersachs *et al.* 2009) may result in high spatial variation of $\delta^{15}N$ of primary producers, and thus of primary consumers.

Yellow perch trophic position

$\delta^{15}N$ indicated a slight increase in trophic position between 0+ perch and other age classes and parasitological data suggested that a diet shift occurred between 0+ and 1+ when, according to parasites, yellow perch switched from zooplanktivory to a diet dominated by benthic invertebrates. No increase of trophic position and no other diet shift occurred between 1+ and 3+. The absence of increase in trophic position revealed by $\delta^{15}N$ indicated that piscivory was low and did not increased with age. While the ontogenetic diet shift from zooplankton to macroinvertebrates between 0+ and 1+ perch appears to be widespread (Whiteside *et al.* 1985; Wu & Culver 1992; Parrish & Margraf 1994), the low rate of piscivory we observed is not as common. Perch may include a large proportion fish in their diet as soon as age 1, while the age at which perch become primarily piscivorous is highly variable among systems, ranging from age 1 to 4 (Fullhart *et al.* 2002; Parker *et al.* 2009), and seems to be determined by the structure of the whole community (Hjelm *et al.* 2000; Svanback & Persson 2004). Our results indicate that in LSP, age 1 to age 3 perch depend on the same resources, that is, benthic invertebrates.

Conclusion

The striking isotopic gradient in LSP allowed us to make inferences about movements of yellow perch in this river-floodplain ecosystem. By comparing perch variability in $\delta^{13}C$ to that of primary consumers, we estimated that the adult perch feeding range was around 3 km on the shore-channel axis. Linear ranges did not increase between 1+, 2+ and 3+ age classes. However, perch $\delta^{15}N$ and trophically-transmitted parasites indicated that no increase of trophic position and no diet shift occurred among these same age classes. These results suggest that the usual increases observed in interspecific allometric relationships between fish home range to body size (e.g. Minns 1995) could be related to trophic position.

Trophically-transmitted parasites revealed that a high proportion of 0+ perch was composed of zooplankton, but that this proportion was small in adults' diet, indicating that zooplanktivory was not a confounding factor in our interpretation of their $\delta^{13}C$. The

combined use of isotopic ratios and parasites allowed us to determine that in LSP, the adult population uses a wide range of habitats between the floodplain and the main channel, but also that individually, each perch exploits restricted areas.

Acknowledgements

We thank A. Gendron for her help in parasitological procedures, R. Bacon, M-E. Deshaies, F. Darchambeau and M. Théberge for their logistic support and assistance in the field, and A-A. Beaudoin, D. Gadbois-Côté , G. Pepin and J. Trépanier for their technological assistance. This study was supported by grants from the Natural Sciences and Engineering Research Council of Canada and the Canada Research Chairs program to PM. and research funds from the St. Lawrence Action Plan (Environment Canada) to DM.

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Table 1 : Total length and standard deviation, mean $\delta^{13}C$ and standard deviation, number of individuals, trophic position (upper letter case shows significant differences, see Methods) and standard deviation, reduced major axis slope, and estimates of linear feeding range (β).

Group	Length (cm)	S. D.	Mean $\delta^{13}C$ (‰)	S. D.	n	TP	S. D.	RMA slope	β (km)
Primary consumer			-24.61	7.7					
Invertebrate predator			-27.66	6.04				0.78	
0+ perch 2005	02.6	0.43	-31.08	1.36	33	3.21 [a]	0.19		
1+ perch 2005	11.8	0.45	-22.20	3.39	58	3.46 [b]	0.28	0.44	3.02
2+ perch 2005	16.1	1.52	-23.18	3.89	182	3.45 [b]	0.25	0.51	2.67
3+ perch 2005	18.9	0.97	-24.24	3.77	54	3.48 [b]	0.29	0.49	2.76
2+ perch 2004	16.9	2.19	-21.09	3.41	72	3.50	0.29	0.44	2.95

Figure legends

Figure 1 : Locations of sampling sites of invertebrates collected in 2004 and 2006 (dots) and yellow perch (*Perca flavescens*) collected in 2004 and 2005 (stars) in Lake Saint-Pierre, Québec, Canada

Figure 2 : Relationship between $\delta^{13}C$ of benthic primary consumers collected in 2004 and 2006 and (a) the distance from the shore, (b) the distance from the channel (km) in Lake St. Pierre, Québec, Canada.

Figure 3 : Relationship between $\delta^{13}C$ of primary consumers and invertebrate predators collected at 23 sampling sites in 2004 in Lake St. Pierre, Québec, Canada. The RMA relationship is shown by the solid line.

Figure 4 : Relationship between $\delta^{13}C$ and $\delta^{15}N$ of 0+ (black circles), 1+, 2+ and 3+ (empty circles) yellow perch (*Perca flavescens*) collected in 2004 and 2005, and of primary consumers (triangles) collected in 2004 and 2006 in Lake St. Pierre, Québec, Canada. Lines represent the tendency curves of a general linear model $\delta^{15}N = \delta^{13}C$ performed on perch, and on primary consumers.

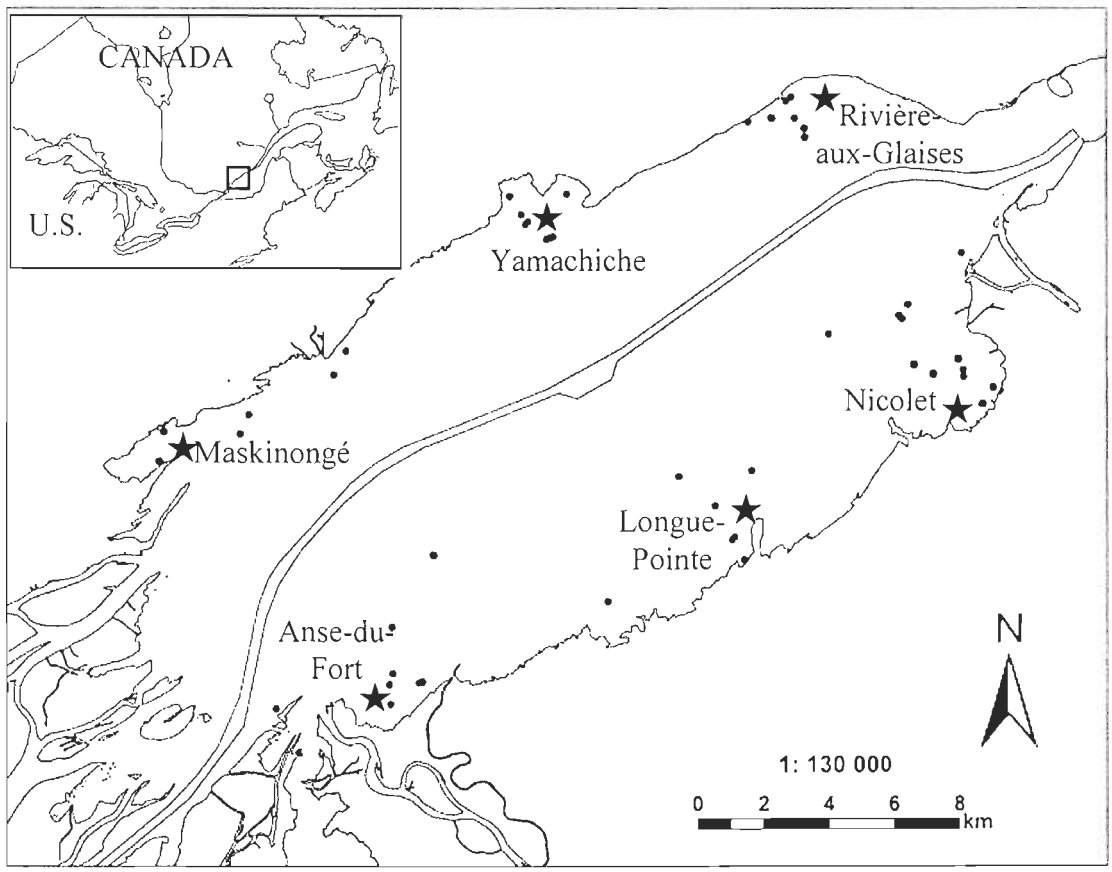
Figure 5 : $\delta^{13}C$ values of 2+-3+ yellow perch (*Perca flavescens*) captured in 2004 (light grey boxes), and of 0+ (dark grey boxes), 1+ (black boxes), 2+ (white boxes), 3+ (dashed boxes) perch captured in 2005 at Maskinongé (Maski), Yamachiche (Yam), Rivière-aux-Glaises (RAG), Anse-du-Fort (ADF), Longue-Pointe (LP), and Nicolet in Lake St. Pierre, Quebec, Canada. Each box enclosed 50% of the data, the lower and upper part of the boxes give the estimated 25^{th} and 75^{th} percentiles, and the line in the middle indicates the median value. The upper and lower whiskers are drawn from the

box to the most extreme point within 1.5 interquartile range. Values between the 1.5 and 3 interquartile ranges are represented by an asterix.

Figure 6 : Relationship between $\delta^{15}N$ of benthic primary consumers collected in 2004 and 2006 and the distance from the channel (km) in Lake St. Pierre, Québec, Canada.

Figure 7 : Mean percent (error bars = S. D.) of parasites transmitted by zooplankton (*Proteocephalus* sp., *Bothriocephalus* sp., *Bunodera sacculata.*; white boxes) and benthic invertebrates (*Raphidascaris acus*, *Crepidostomum cornutum*, *Phyllodistomum superbum*, *Neoechinorhynchus rutili*, *Echinorhynchus lateralis*; grey boxes) in 0+, 1+, 2+ and 3+ yellow perch (*Perca flavescens*) from the six sampling sites in Lake St. Pierre, Québec, Canada (2004-2005).

Figure 8 : Relationship between the percent of parasite individuals transmitted by zooplankton in perch and $\delta^{13}C$ of 0+ (black circles), 1+ (squares), 2+ (triangles), and 3+ (empty circles) yellow perch (*Perca flavescens*) captured in 2004 and 2005 at Maskinongé, Yamachiche, Rivière-aux-Glaises, Anse-du-Fort, Longue-Pointe, and Nicolet in Lake St. Pierre, Québec, Canada.


CANADA
U.S.
Rivière-
aux-Glaises
Yamachiche
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0 2 4 6 8
km

Figure 1

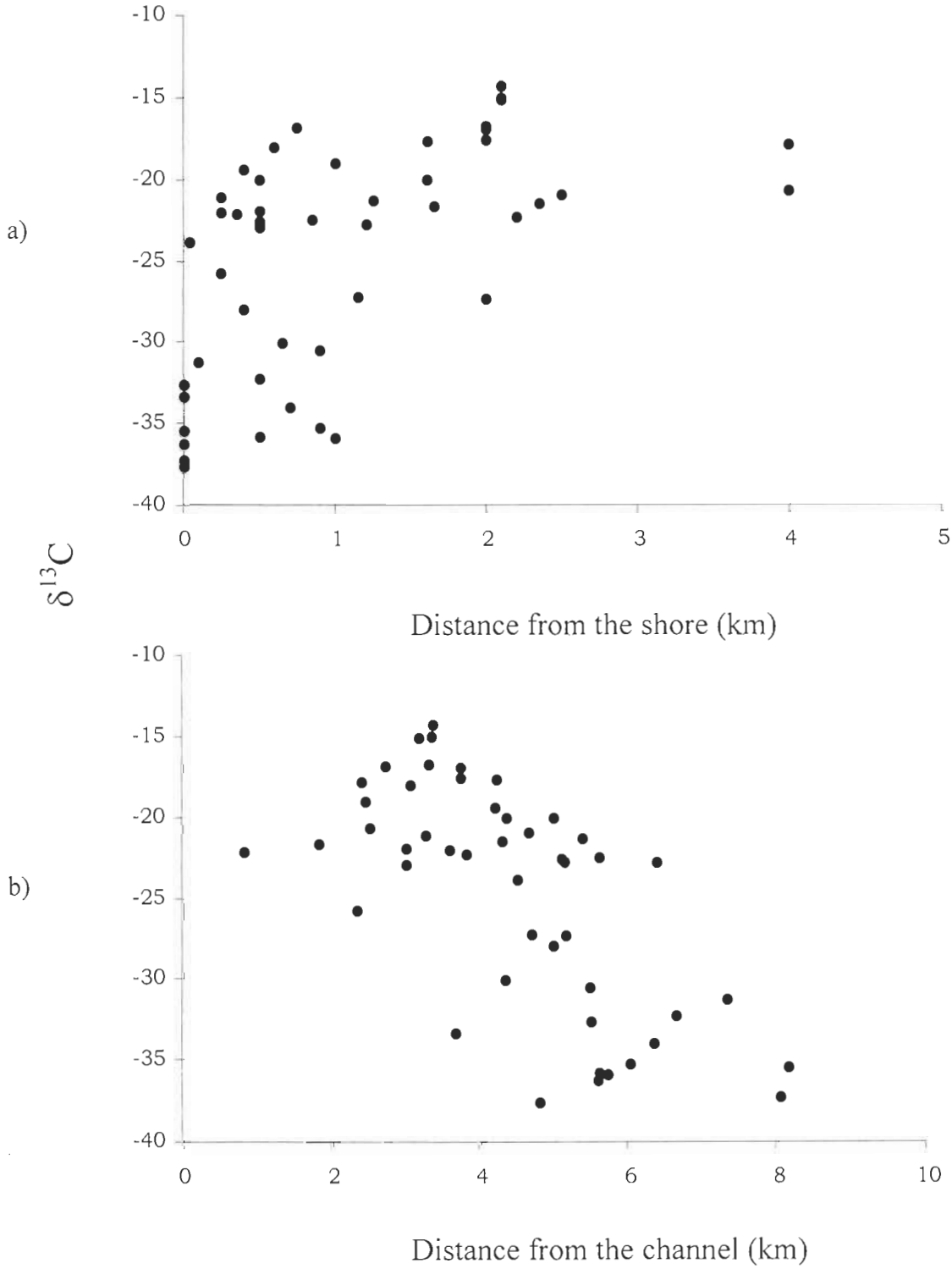
a)
-10
-15
-20
-25
-30
-35
-40
0
1
2
3
4
5
δ13C
Distance from the shore (km)
b)
-10
-15
-20
-25
-30
-35
-40
0
2
4
6
8
10
Distance from the channel (km)

Figure 2

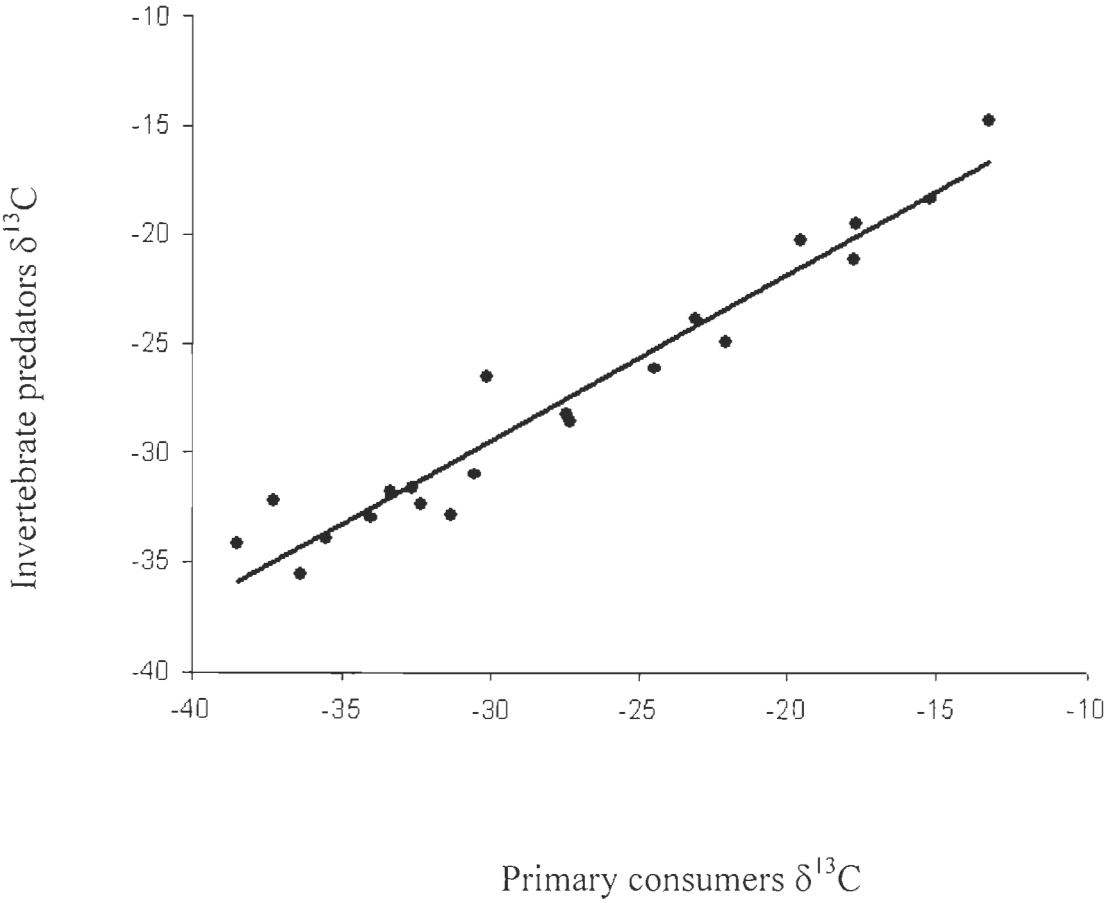
-10
-15
-20
-25
-30
-35
-40
-40
-35
-30
-25
-20
-15
-10
Invertebrate predators δ13C
Primary consumers δ13C

Figure 3

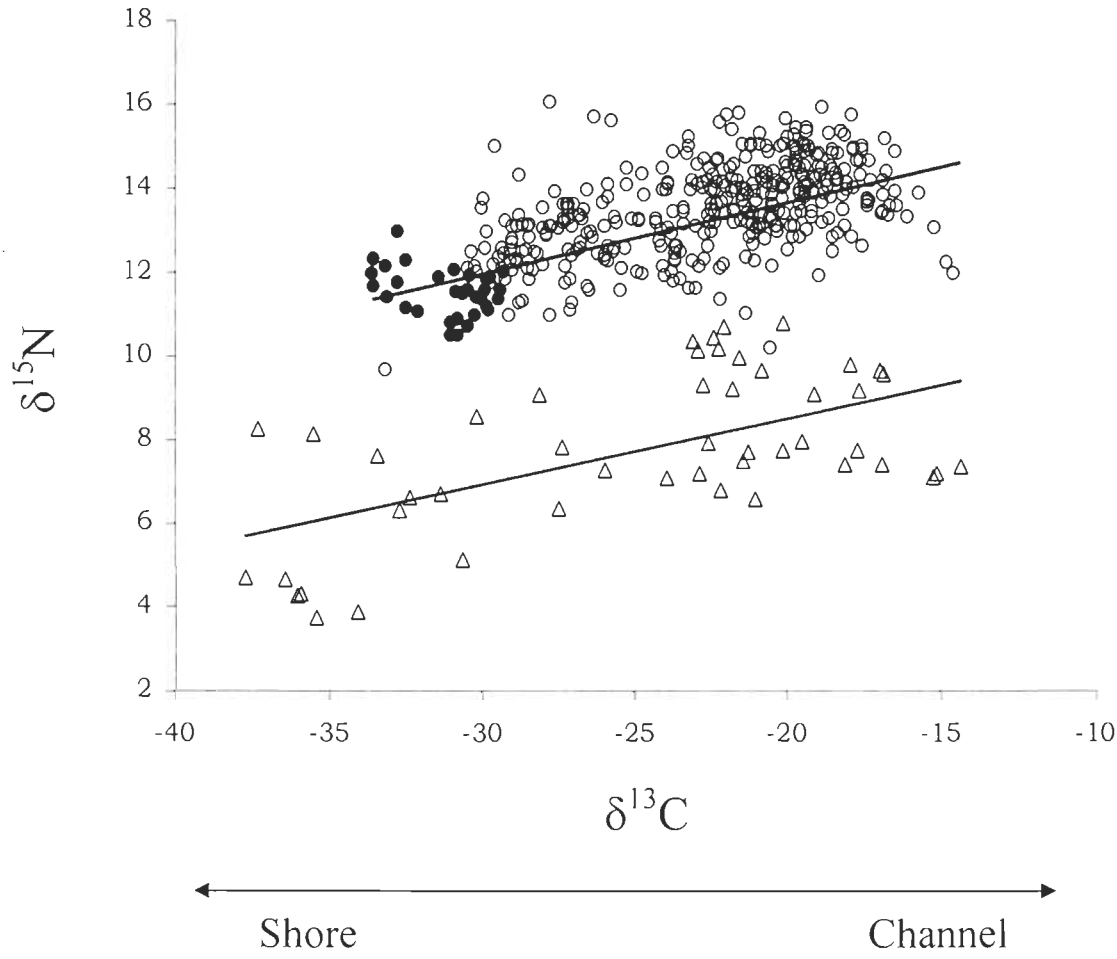

Figure 4

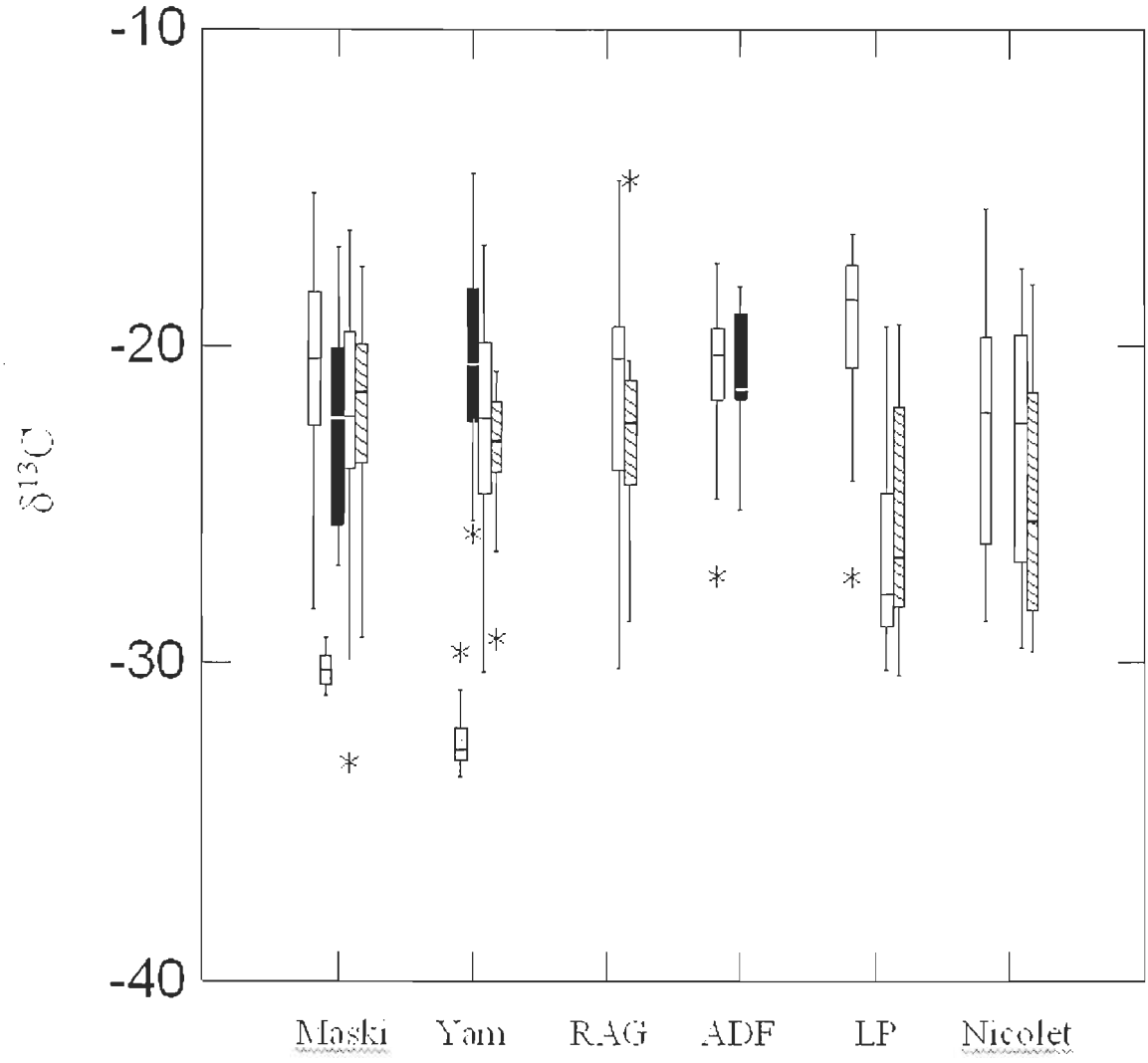

Figure 5

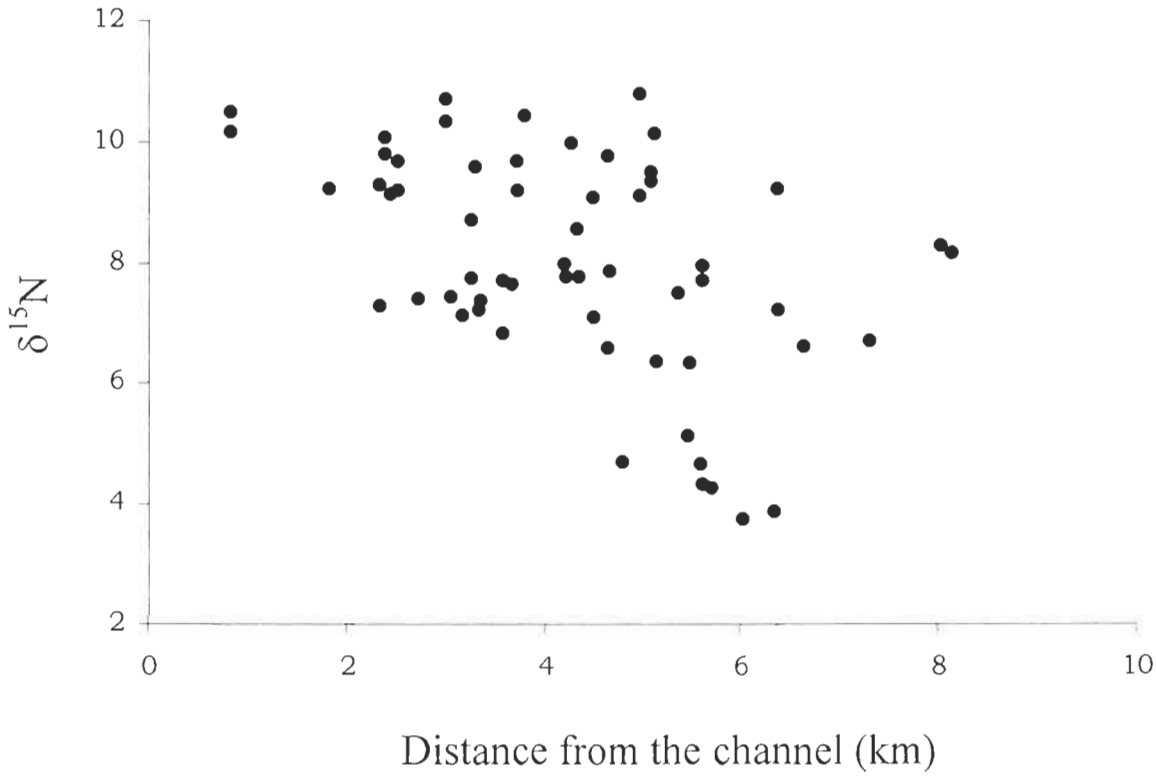

Figure 6

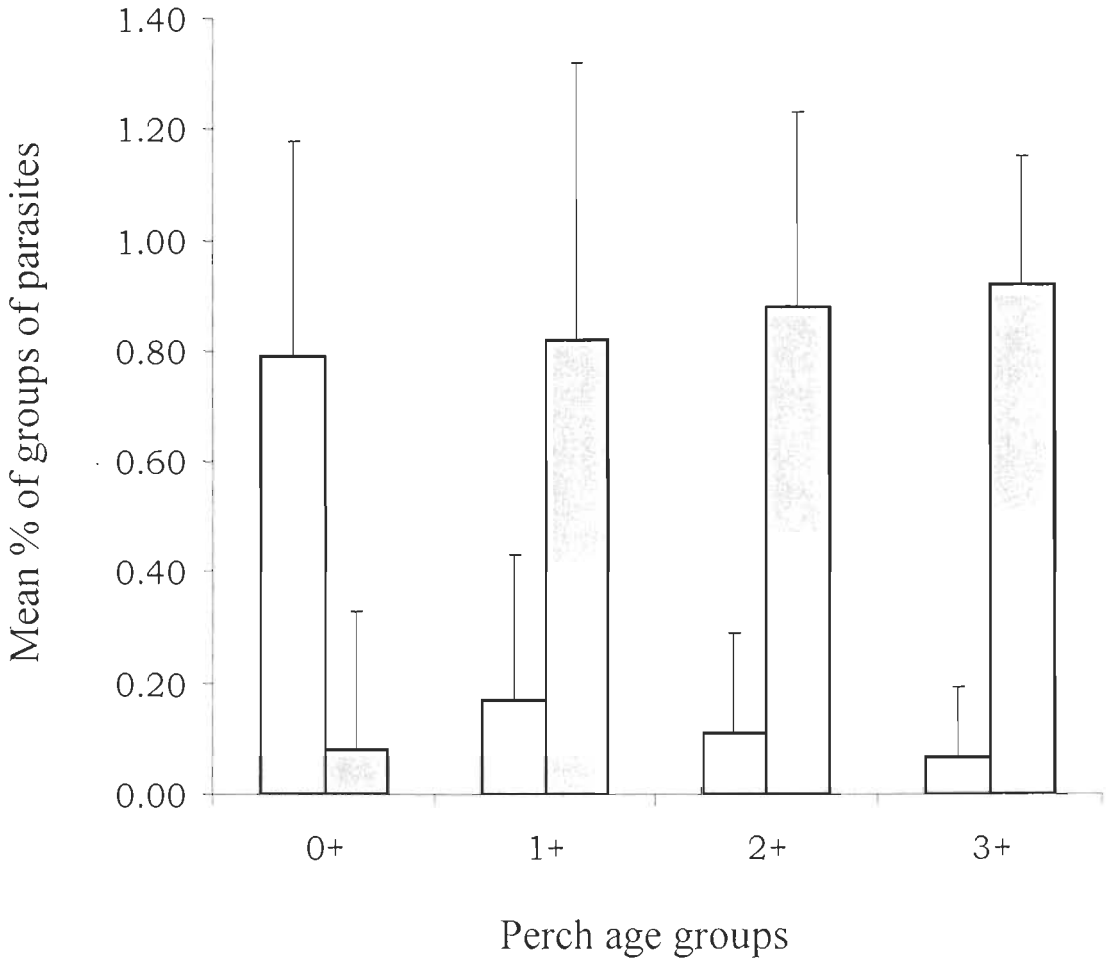
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
Mean % of groups of parasites
0+
1+
2+
3+
Perch age groups

Figure 7

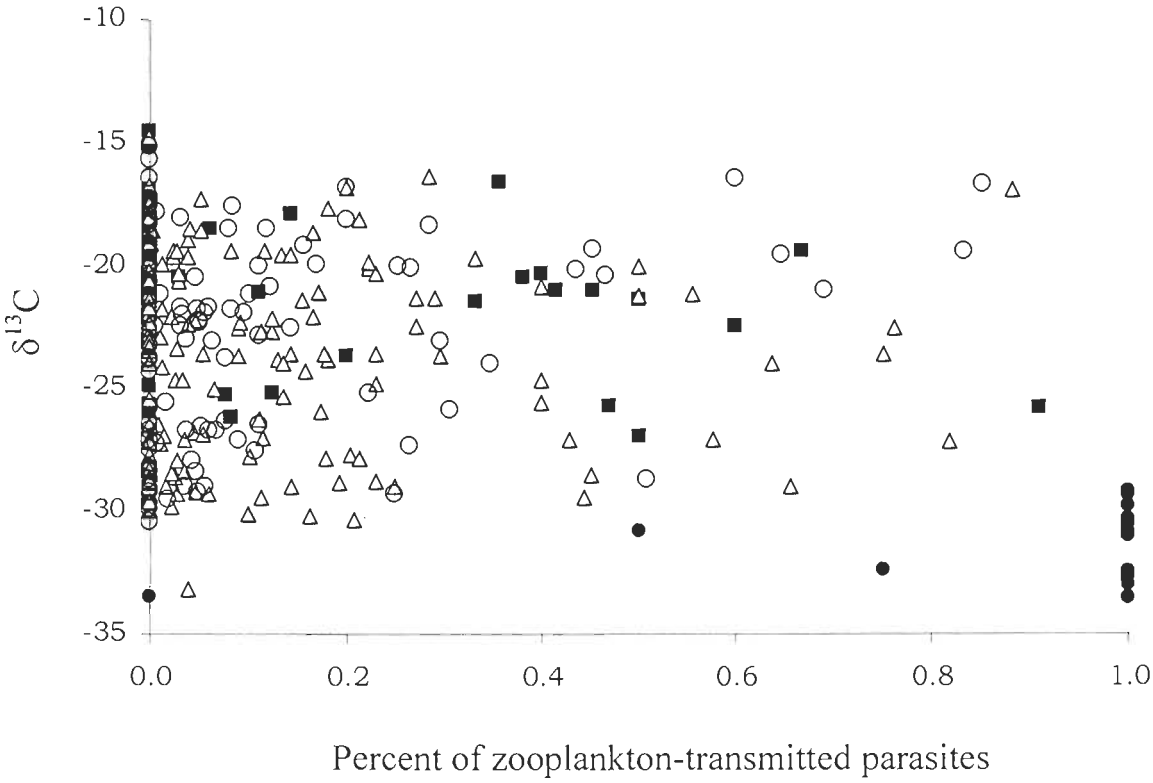
-10
-15
-20
-25
-30
-35
δ13C
0.0
0.2
0.4
0.6
0.8
1.0
Percent of zooplankton-transmitted parasites

Figure 8

CONCLUSION GÉNÉRALE

Les marais aménagés, initialement conçus pour être des habitats de reproduction et d'alimentation pour la sauvagine, sont rapidement devenus intéressants pour un grand nombre d'espèces. Par exemple, au marais aménagé de la baie de Lavallière, situé dans la plaine inondable du lac Saint-Pierre, plus de 80 espèces d'oiseaux, 27 espèces de poisson, 20 espèces de mammifères et 10 espèces d'amphibiens y ont déjà été recensés (Foucrier *et al.* 2007). Toutefois, leur mode de gestion a récemment été remis en question et a fait l'objet d'études destinées notamment à établir des recommandations à cet effet (Lepage et Lalumière 2003, Kaminski *et al.* 2006, Foucrier *et al.* 2007, Nedland *et al.* 2007). Par exemple, l'observation d'une mortalité élevée de poissons après l'hiver et d'une modification importante de la composition de la communauté végétale au fil des ans suggère que l'absence de fluctuations des niveaux d'eau et la présence de structures de rétention d'eau peuvent avoir des effets considérables sur la faune et la flore (Lepage et Lalumière 2003, Foucrier *et al.* 2007).

Nous avons observé des différences notables entre les parasites des perchaudes juvéniles provenant deux marais aménagés, où des digues et des barrages maintiennent le niveau d'eau stable, et les parasites de perchaudes juvéniles provenant deux marais naturels du lac Saint-Pierre. La similarité de la communauté de parasites était plus grande à l'intérieur qu'entre les deux types de marais. De plus, la richesse spécifique et la diversité des parasites étaient plus élevées dans les marais naturels que dans les marais aménagés. Les glochidies, le stade larvaire des moules Unionidae, ainsi que *Bunodera* sp. et *Crepisostomum* sp., des digènes transmis par des moules Sphaeridae, étaient absents des marais aménagés. Aucune relation n'a été observée entre la taille ou le poids des poissons et la diversité de leurs parasites, ainsi qu'entre la distance qui séparait les sites à l'étude et la similarité des communautés de parasites. Ces résultats suggèrent que la différence de parasites observée entre les deux types de marais est due à des facteurs locaux qui structurent les habitats et déterminent la communauté des hôtes des parasites.

Les différences de connectivité et de fluctuation des niveaux d'eau entre les deux types de marais pourraient expliquer ces différences de faune parasitaire. Dans les marais aménagés, les faibles fluctuations du niveau d'eau et la courte période de contact avec les eaux du Saint-Laurent limitent l'action érosive qu'exercent les glaces et les forts débits. Cette situation favorise l'établissement de quelques espèces végétales de grande taille et le développement d'un substrat essentiellement composé de rhizomes ancrés dans un mélange de sédiments et de matière organique en décomposition (Foucrier *et al.* 2007). En effet, les structures de rétention d'eau favorisent l'emprisonnement des sédiments transportés à l'intérieur des marais pendant les crues printanières (Tockner *et al.* 1999, Svendsen *et al.* 2009).

L'absence des deux digènes *Bunodera* sp. et *Crepidostomum* sp. et celle des glochidies dans les marais aménagés peut s'expliquer par la fragilité de ces organismes et des hôtes impliqués dans leur cycle de vie. Les oeufs et le stade larvaire libre des digènes sont sensibles aux caractéristiques chimiques et physiques des habitats telles que la température, le pH, la lumière, et la dessiccation (Pietrock et Marcogliese 2003). Par ailleurs, les moules Unionidae sont parmi les premières espèces benthiques à disparaître lorsque la qualité de l'habitat se dégrade (Bogan 1993). Dans les marais aménagés, la combinaison d'un taux de sédimentation élevé et une faible concentration en oxygène, due à la décomposition de l'importante biomasse végétale (Foucrier *et al.* 2007), pourraient avoir un effet négatif sur les bivalves qui sont des organismes filtreurs, peu tolérants aux faibles concentrations en oxygène et à la siltation (Popp et Hoagland 1995, Burlakova et Karatayev 2007).

Compte tenu de la relation qui existe entre la diversité des parasites et celle des hôtes impliqués dans leur cycle de vie (Simková *et al.* 2003, Hechinger et Lafferty 2005, Hechinger *et al.* 2007), il est probable que la diversité plus élevée des parasites des perchaudes vivant dans les marais naturels soit le reflet d'un réseau trophique plus élaboré que celui des marais aménagés. En réduisant la connectivité et les fluctuations des niveaux d'eau, les structures de rétention d'eau peuvent avoir un impact négatif sur les habitats de plusieurs espèces et résulter en un réseau trophique simplifié.

D'importantes frayères de perchaudes sont situées dans marais naturels du lac Saint-Pierre. Jusqu'à tout récemment, soit avant l'adoption de mesures restrictives visant à protéger la population, l'essentiel des captures annuelles de perchaudes par les pêcheurs commerciaux avait lieu pendant la période de fraye (Magnan 2002). C'est ainsi que les perchaudes qui ont servi à notre étude ont été prélevées en 2004 et 2005 sur les sites de fraye de six secteurs (Maskinongé, Yamachiche, Rivière-aux-Glaises, Anse-du-Fort, Longue-Pointe, Nicolet), à même les captures des pêcheurs commerciaux, à l'exception du site de Rivière-aux-Glaises, où il n'y avait pas de pêcheurs et où nous avons dû effectuer les captures. Il est à noter qu'à chaque site, les perchaudes de grandes tailles étaient rares. De ce fait, nos analyses ont été réalisées avec des individus dont l'âge n'excédait pas 3+. Nous avons également capturé, à la fin juin 2005, des perchaudes âgées d'environ 5 semaines (classe d'âge 0+) dans les secteurs Maskinongé et Yamachiche. La distance minimale entre les sites sélectionnés était d'environ 10 km. Nous avons utilisé les parasites et le $\delta^{13}C$ pour déterminer les patrons spatiaux de la population de perchaudes. Nos résultats suggèrent que (i) les perchaudes 0+ à 3+ demeurent fidèles à un secteur, et (ii) après la période de fraye, les perchaudes adultes se dispersent dans le lac et par la suite, du moins pendant la saison de croissance, l'étendue de l'habitat d'alimentation de chaque individu sur l'axe rive-chenal est de l'ordre de 3 km. L'ensemble de ces résultats est présenté de façon schématique à la figure 1.

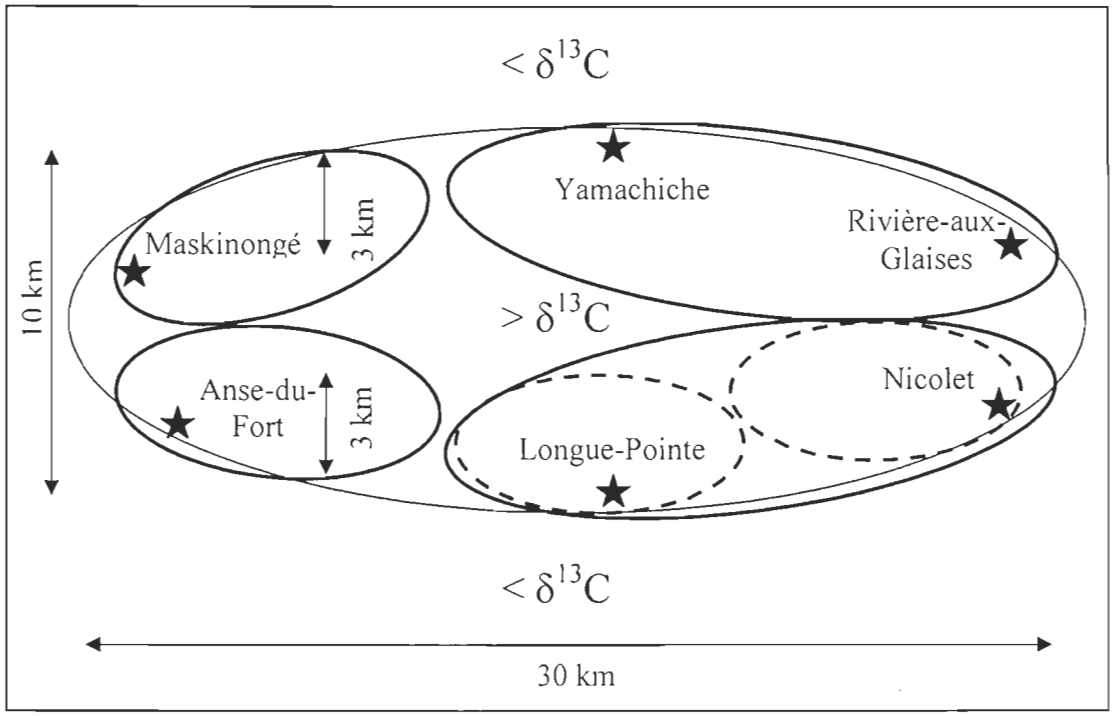

Figure 1 : Représentation schématique du lac Saint-Pierre, des sites de capture des adultes (étoiles), des groupes distingués par les parasites (formes aux traits foncés, continus) et des groupes distingués par le $\delta^{13}C$ des perchaudes (formes aux traits pointillés). Les flèches verticales représentent l'étendue approximative de l'habitat d'alimentation des perchaudes 1+-3+ (3 km). Sur chaque rive, une distance approximative de 10 km sépare les sites de capture des perchaudes.

Afin de déterminer si la population était constituée de plus d'un stock, nous avons examiné s'il y avait des différences au niveau des parasites et du $\delta^{13}C$ des perchaudes 0+ à 3+ provenant des différents secteurs du lac. Chez les perchaudes 1+ et 2+-3+, les analyses canoniques de variance réalisées avec les parasites ont distingué quatre groupes, soit le groupe Maskinongé, le groupe Yamachiche - Rivière-aux-Glaises, le groupe Anse-du-Fort, et le groupe Longue-Pointe - Nicolet. De plus, une analyse de variance révélait que le $\delta^{13}C$ des perchaudes de Longue-Pointe était plus négatif que

celui des perchaudes de Nicolet, suggérant que ces deux groupes étaient distincts. Quant aux perchaudes 0+, autant les parasites que le $\delta^{13}C$ distinguaient celles de Maskinongé de celles de Yamachiche. C'est ainsi que, conjointement, les deux marqueurs ont permis de distinguer cinq groupes. Nos résultats suggèrent que les groupes formés lors de la période de reproduction demeurent distincts au moins jusqu'à ce que les perchaudes aient atteint l'âge 3+. De plus, le fait que certains des parasites retenus par les analyses, notamment *Diplostomum* spp. et *Raphidascaris acus*, peuvent vivre plus d'un an dans les poissons, et que *Diplostomum* spp., *Crepidostomum cornutum* et *Echinorhynchus lateralis* discriminaient les mêmes sites en 2004 et en 2005, indique une fidélité au site depuis au moins deux ans.

D'autre part, les conditions environnementales contrastantes qui existent entre les masses d'eau qui coulent près des rives et celle qui coule au centre du lac nous ont permis d'estimer l'étendue de l'habitat d'alimentation des perchaudes adultes du lac Saint-Pierre. Dû à son équilibre avec le carbone atmosphérique et à son contact avec des sédiments riches en carbonates, la masse d'eau centrale a des valeurs de δ^{13}_{DIC} moins négatives que les masses d'eau qui coulent le long des rives (Yang *et al.* 1996, Barth et Veizer 1999). De plus, les eaux peu profondes en bordure du lac sont caractérisées par une concentration élevée en carbone organique dissous et un long temps de résidence (Hudon et Carignan 2008), favorisant des taux élevés de décomposition et de respiration bactérienne (Welcomme 1979). Ces conditions peuvent résulter en de faibles valeurs du δ^{13}_{DIC} (Fourqurean *et al.* 1997, Keough *et al.* 1998, Barth et Veizer 1999).

Nous avons examiné le $\delta^{13}C$ d'invertébrés benthiques peu mobiles, capturés à 48 sites répartis dans l'ensemble du lac, relativement à leur distance de la rive et du chenal. Sur l'axe rive-chenal, le $\delta^{13}C$ des invertébrés benthiques peu mobiles était très variable et suivait un fort gradient, les valeurs très négatives étant observées près des rives et les moins négatives près du chenal. Ces résultats suggèrent que le $\delta^{13}C$ d'un individu reflète sa position spatiale le long de l'axe latéral au lac Saint-Pierre. La comparaison de la variabilité du $\delta^{13}C$ des perchaudes et des consommateurs primaires nous a permis

d'estimer que l'étendue de l'habitat d'alimentation des perchaudes 1+-3+ était de l'ordre de 3 km, quelque soit leur âge ou leur taille, qui variait de 6.5 à 21.4 cm les trois classes d'âge réunies. Ces résultats sont inattendus compte tenu de la relation allométrique bien connue entre la taille d'un individu et l'étendue de son domaine vital (ex : Kramer et Chapman 1999) ou de son habitat d'alimentation (ex : Peters 1983, Minns 1995). Nos résultats s'expliquent possiblement par le fait qu'il ne semble pas y avoir d'augmentation de position trophique entre les perchaudes 1+ et 3+. En effet, les analyses réalisées avec leur $\delta^{15}N$ indiquaient que la seule augmentation de position trophique entre les classes d'âge considérées dans l'étude avait lieu entre les perchaudes 0+ et 1+. De plus, l'examen des parasites transmis par l'alimentation révélait qu'il y n'avait qu'un seul changement important de régime alimentaire, soit entre les perchaudes 0+, essentiellement zooplanctivores, et les perchaudes 1+ qui, comme les perchaudes 2+ et 3+, se nourrissaient principalement d'invertébrés benthiques. Ces résultats suggèrent que l'étendue de l'habitat d'alimentation d'un individu pourrait être plus fortement influencée par sa position trophique que par sa taille. Nos résultats indiquent qu'individuellement, les perchaudes du lac Saint-Pierre s'alimentent à l'intérieur d'un territoire relativement restreint, mais que l'ensemble de la population se distribue dans une bonne partie du lac.

Perspectives de recherche

Malgré le fait que plusieurs études se soient intéressé aux patrons spatiaux de la perchaude, une incertitude demeure toujours quant à l'importance de ses déplacements. En effet, alors que certaines études suggèrent soit une fidélité au site (Aalto et Newsome 1989), soit une population spatialement structurée (Guénette *et al.* 1994, Tardif *et al.* 2005), d'autres études rapportent des déplacements sur plus de 100 km (Dumont 1996, de Lafontaine *et al.* 2006). De plus, une étude de marquage et recapture de perchaudes du lac Saint-Pierre (Leclerc 1987) suggéraient que non seulement certaines perchaudes effectuaient des déplacements importants à l'intérieur du lac Saint-Pierre, mais aussi que certaines traversaient le chenal de navigation. À titre d'exemple, quelques perchaudes marquées au secteur de l'Anse-du-Fort avaient été retrouvées au secteur de la Rivière-

aux-Glaises (Leclerc 1987). Nos résultats suggèrent que les perchaudes d'âge 1+ à 3+ se déplacent relativement peu sur l'axe latéral au lac Saint-Pierre. Sur l'axe longitudinal, la seule information qui nous permette d'estimer leurs déplacements est celle suggérée par leur fidélité au site de capture. Ceux-ci étant approximativement équidistants de 10 km, nous pouvons estimer que c'est la distance maximale qu'elles parcourent sur l'axe longitudinal. Nous ne pouvons toutefois exclure la possibilité que certaines perchaudes aient effectué des déplacements plus importants.

Un contraste frappant entre l'étude de Dumont (1996), réalisée au lac Saint-Louis, un autre lac fluvial du Saint-Laurent, celle de Leclerc (1987) et la nôtre, est la taille et/ou l'âge des perchaudes qui ont servi aux études. Dans l'étude de marquage et recapture de Dumont (1996) qui s'est déroulée de 1988 à 1990, la longueur et l'âge moyens des perchaudes étaient respectivement de 17.7 à 20 cm et 3.7 à 5.2 ans, pour un effectif de près de 500 individus. Dans celle de Leclerc (1987), réalisée de 1978 à 1980, la longueur moyenne des perchaudes était de 19.3 à 22.9 cm, pour un effectif de plus de 1000 poissons. Dans notre étude, la longueur moyenne des perchaudes était 16.4 cm et leur âge moyen était 2.0 ans, pour un effectif de 382 poissons. Si, la taille (Peters 1983, Minns 1995, Kramer et Chapman 1999) ou, comme le suggérait notre étude, la position trophique d'un individu influence l'étendue de ses déplacements, les différences de taille et d'âge pourraient expliquer les différences de résultats entre les études.

La différence entre la taille moyenne des perchaudes de l'étude de Leclerc (1987) et celles de notre étude est particulièrement intéressante à comparer puisque les deux études ont été réalisées au lac Saint-Pierre et que l'échantillonnage a été fait de la même façon, c'est-à-dire à partir des captures des pêcheurs commerciaux. Comme il a été mentionné auparavant, les perchaudes de grandes tailles étaient très rares lors de notre échantillonnage, en 2004 et 2005. Étant donné que la pêche intensive a généralement pour effet de soustraire les individus de plus grandes tailles (Anderson *et al.* 2008, Glover *et al.* 2008), donc ceux qui peuvent occuper une position trophique élevée, l'exploitation intensive de la perchaude au lac Saint-Pierre a peut-être eu pour effet d'éliminer les grands individus qui sont plus mobiles. L'examen de 50 ans de données a

démontré que la suppression des classes d'âge élevées suivant l'exploitation intense d'une population a pour effet de réduire la stabilité de la population (Anderson *et al.* 2008). Les grands poissons répondent mieux aux fluctuations environnementales, notamment grâce à leur plus grande mobilité qui leur permet d'éviter les secteurs de qualité inférieure (Anderson *et al.* 2008).

Notre étude suggère que la population de perchaudes du lac Saint-Pierre est composée d'individus relativement peu mobiles, se nourrissant tous d'organismes d'un même niveau trophique. Si l'absence de perchaudes de grande taille est le résultat d'une exploitation intensive, la structure actuelle de la communauté aquatique pourrait être modifiée au cours des prochaines années. En effet, les lacs peu profonds sont particulèrement vulnérables aux changements de régime, ceux-ci pouvant, par exemple, passer de façon radicale de l'état d'eau claire à l'état d'eau turbide (Scheffer et Carpenter 2003, Folke *et al.* 2004, van de Meutter *et al.* 2005). Le lac Saint-Pierre pourrait ainsi atteindre un état stable différent de son état actuel, non désirable et difficile à renverser (Scheffer et Carpenter 2003). Seul un suivi serré de l'ensemble de la communauté aquatique pourrait détecter que le système est près d'atteindre un seuil critique et permettre d'élaboration de recommandations appropriées.

Grâce à ses propriétés exceptionnelles, le lac Saint-Pierre nous a offert la possibilité de tester certaines hypothèses visant à mieux comprendre les facteurs impliqués dans la structuration spatiale et l'intégrité écologique de sa population de perchaudes. L'hétérogénéité des caractéristiques physiques, chimiques et biologiques du lac est très grande. Par exemple, l'étendue des valeurs du $\delta^{13}C$ des consommateurs primaires que nous avons observée sur moins de cinq km est supérieure à celle observé à l'échelle continentale par Finlay (2001). Par ailleurs, l'hétérogénéité spatiale des habitats est suffisamment importante pour qu'on puisse observer des différences de parasites chez des perchaudes capturées à 10 km de distance. De plus, la diversité de ses milieux humides et l'importance de l'étendue qu'ils occupent ont permis de comparer les parasites des perchaudes provenant de marais aménagés et naturels. D'autres systèmes affichent des caractéristiques semblables à celles du lac Saint-Pierre. Par exemple, le

contraste entre les masses d'eau en terme de qualité chimique et optique est comparable à celui observé, par exemple, à la confluence du fleuve Amazone et du Rio Negro (Aucour *et al.* 2003, Moreira-Turcq *et al.* 2003) ou encore du Nil Blanc et du Nil Bleu (Sinada et Karim 1984). Par ailleurs, d'importantes plaines inondables se retrouvent en bordure de la plupart des grandes rivières. Mais ce qui fait du lac Saint-Pierre un site d'étude d'une grande valeur est qu'il rassemble toutes ces caractéristiques.

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ANNEXE 1

$\delta^{13}C$ et $\delta^{15}N$ des invertébrés récoltés en 2004 au lac Saint-Pierre, location géographique, distance de la rive et du chenal de leurs sites de capture.

Invertébrés	$\delta^{13}C$	$\delta^{15}N$	Longitude	Latitude	Distance de la rive (km)	Distance du chenal (km)
Chironomid	-37.38	8.18	72° 39′ 20,0″ W	46° 12′ 22,0″ N	0.05	8.05
Gammarus sp.	-37.25	8.32				
Amphiagrion sp.	-32.21	7.86				
Amnicola sp.	-35.11	8.03	72° 39′ 19,1″ W	46° 12′ 15,7″ N	0.05	8.15
Chironomid	-35.92	8.25				
Amphiagrion sp.	-33.95	8.50				
Amnicola sp.	-26.79	5.25	72° 40′ 53,2″ W	46° 12′ 34,3″ N	2.00	5.16
Chironomid	-30.23	8.21				
Gammarus sp.	-26.34	5.99				
Amphiagrion sp.	-28.36	7.08				
Amnicola sp.	-36.24	3.68	72° 40′ 09,4″ W	46° 12′ 30,6″ N	0.90	6.03
Chironomid	-34.50	3.75				
Amnicola sp.	-35.55	3.47	72° 40′ 09,4″ W	46° 12′ 37,5″ N	1.00	5.72
Chironomid	-37.36	5.46				
Gammarus sp.	-35.03	3.85				
Amnicola sp.	-29.08	5.47	72° 40′ 15,7″ W	46° 12′ 48,2″ N	0.90	5.48
Chironomid	-36.27	6.11				
Gammarus sp.	-30.18	4.42				
Amphiagrion sp.	-30.98	5.90				
Amnicola sp.	-15.96	9.62	72° 41′ 26,4″ W	46° 13′ 43,5″ N	2.00	3.30
Chironomid	-16.36	9.89				
Gammarus sp.	-18.70	8.93				
Amnicola sp.	-16.97	9.36	72° 41′ 34,9″ W	46° 13′ 29,5″ N	2.00	3.73
Chironomid	-18.38	9.00				
Amphiagrion sp.	-19.53	12.26				
Amnicola sp.	-16.40	9.46	72° 41′ 39,3″ W	46° 13′ 33,0″ N	2.00	3.73
Chironomid	-16.89	9.66				

Gammarus sp.	-17.69	9.85				
Amnicola sp.	-27.50	5.17	72° 45′ 29,5″ W	46° 09′ 37,5″ N	0.10	7.32
Chironomid	-34.93	8.09				
Gammarus sp.	-31.74	6.94				
Amphiagrion sp.	-32.86	8.75				
Amnicola sp.	-31.55	5.75	72° 45′ 45,8″ W	46° 09′ 57,5″ N	0.50	6.65
Chironomid	-34.12	7.78				
Gammarus sp.	-31.36	6.27				
Amphiagrion sp.	-32.34	8.07				
Amnicola sp.	-21.49	7.71	72° 46′ 08,5″ W	46° 10′ 31,3″ N	-21.43	5.38
Chironomid	-20.57	8.71				
Gammarus sp.	-21.81	6.60				
Amnicola sp.	-20.38	10.34	72° 46′ 58,5″ W	46° 11′ 00,9″ N	-21.56	4.29
Chironomid	-21.47	10.26				
Gammarus sp.	-22.20	9.65				
Amnicola sp.	-34.40	4.28	72° 45′ 41,9″ W	46° 10′ 00,5″ N	-34.03	6.35
Chironomid	-35.06	3.67				
Gammarus sp.	-32.82	3.83				
Amphiagrion sp.	-32.96	5.10				
Amnicola sp.	-32.08	7.03	72° 53′ 11,7″ W	46° 07′ 31,9″ N	0.05	5.49
Chironomid	-34.28	5.69				
Gammarus sp.	-29.72	6.87				
Amphiagrion sp.	-31.60	8.44				
Amnicola sp.	-29.70	8.42	72° 53′ 57,8″ W	46° 07′ 26,1″ N	0.65	4.33
Chironomid	-30.57	8.67				
Amphiagrion sp.	-26.54	10.96				
Amnicola sp.	-20.15	10.65	72° 53′ 54,0″ W	46° 07′ 56,1″ N	0.50	4.99
Chironomid	-20.06	10.91				
Amnicola sp.	-21.68	9.55	72° 53′ 16,9″ W	46° 07′ 46,5″ N	0.50	5.14
Chironomid	-24.05	10.65				
Gammarus sp.	-24.22	10.74				
Amnicola sp.	-22.40	10.24	72° 53′ 53,2″ W	46° 08′ 41,1″ N	2.20	3.80
Chironomid	-22.07	11.31				
Gammarus sp.	-22.61	9.73				
Amnicola sp.	-36.76	3.85	72° 50′ 48,3″ W	46° 15′ 41,0″ N	0.50	5.62
Chironomid	-34.18	5.32				
Gammarus sp.	-36.81	3.78				
Amnicola sp.	-17.07	7.82	72° 50′ 27,2″ W	46° 15′ 12,8″ N	1.60	4.22
Chironomid	-19.65	7.96				
Gammarus sp.	-16.46	7.45				

Amphiagrion sp.	-21.14	8.27				
Amnicola sp.	-19.89	8.35	72° 50′ 23,6″ W	46° 15′ 15,3″ N	1.60	4.35
Chironomid	-20.01	8.23				
Gammarus sp.	-20.44	6.61				
Amnicola sp.	-13.95	7.75	72° 49′ 57,7″ W	46° 14′ 57,5″ N	2.10	3.35
Chironomid	-14.92	6.97				
Gammarus sp.	-14.17	7.36				
Amnicola sp.	-14.15	7.98	72° 49′ 52,8″ W	46° 14′ 58,9″ N	2.10	3.33
Chironomid	-15.02	7.04				
Gammarus sp.	-16.28	6.54				
Amnicola sp.	-13.58	7.89	72° 49′ 48,8″ W	46° 14′ 59,9″ N	2.10	3.17
Chironomid	-15.18	7.05				
Gammarus sp.	-16.87	6.33				
Amphiagrion sp.	-18.37	8.33				
Amnicola sp.	-26.89	8.41	72° 50′ 33,1″ W	46° 15′ 22,6″ N	1.15	4.68
Chironomid	-26.96	8.58				
Gammarus sp.	-27.75	7.18				
Amphiagrion sp.	-28.58	9.24				
Amnicola sp.	-22.01	10.75	72° 44′ 11,8″ W	46° 17′ 06,9″ N	0.50	2.99
Chironomid	-23.94	10.62				
Gammarus sp.	-23.30	9.66				
Amphiagrion sp.	-23.83	12.28				
Amnicola sp.	-21.66	11.21	72° 44′ 04,2″ W	46° 17′ 10,5″ N	0.50	3.00
Chironomid	-22.69	10.60				
Gammarus sp.	-21.93	10.47				
Amphiagrion sp.	-24.93	11.58				
Amnicola sp.	-20.22	8.90	72° 43′ 46,2″ W	46° 16′ 30,5″ N	1.65	1.83
Chironomid	-23.27	9.50				
Amnicola sp.	-16.65	7.73	72° 44′ 00,1″ W	46° 16′ 49,5″ N	0.75	2.72
Chironomid	-16.40	7.53				
Gammarus sp.	-17.37	7.16				
Amnicola sp.	-35.61	5.53	72° 44′ 27,8″ W	46° 17′ 12,9″ N	0.05	3.66
Chironomid	-36.98	8.47				
Gammarus sp.	-28.75	7.79				
Amphiagrion sp.	-31.80	10.17				
Amnicola sp.	-18.58	10.03	72° 43′ 46,6″ W	46° 16′ 39,3″ N	1.00	2.44
Chironomid	-18.17	9.66				
Gammarus sp.	-19.80	8.36				
Amnicola sp.	-38.32	5.52	72° 59′ 11,7″ W	46° 12′ 07,4″ N	0.05	5.60
Chironomid	-33.56	4.69				

Gammarus sp.	-40.11	3.72				
Amphiagrion sp.	-35.57	5.85				
Chironomid	-38.48	5.33	72° 59′ 12,6″ W	46° 11′ 26,3″ N	0.05	4.81
Gammarus sp.	-36.92	4.03				
Amphiagrion sp.	-34.20	6.44				
Amnicola sp.	-16.36	8.00	72° 57′ 09,7″ W	46° 12′ 13,7″ N	0.40	4.20
Chironomid	-22.20	8.70				
Gammarus sp.	-20.02	7.15				
Amphiagrion sp.	-20.26	9.22				
Amnicola sp.	-17.97	8.33	72° 55′ 07,3″ W	46° 12′ 50,5″ N	0.60	3.06
Chironomid	-16.84	7.90				
Gammarus sp.	-18.78	6.70				